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A STUDY OF THE RESPONSES OF RODENTS TO MONOCHROMATIC LIGHT

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The following study on the responses of rodents to monochromatic light was begun in January, 1911 and was completed in May, 1912. Experiments were discontinued in the summer of 1911. From every standpoint the experiments are far from being satisfactory. It is believed, however, it may be said at the outset, that this paper offers some clear evidence that a differential response on the basis of wave length is not possible in the case of the rat. The tests (in Experiment II) upon the rabbits were never completed. The results of what tests we gave them are so similar to those obtained from the rats that we believe that the total outcome of the work on the rabbits would have been essentially the same as that reported for the rats.

The experiments were made with the color apparatus essentially as it is described in Yerkes and Watson's monograph [1] and by the two color discrimination method there suggested. The discrimination method is in such general use that no description of it is necessary.

EXPERIMENT I

January 11, 1911–June 15, 1911.

The two stimulus lights were *red* (λ=6550) and *green* (λ=5050). In this first experiment the two bands were not equated in energy. They were projected directly upon the plaster surface as they came from the selecting slit. Only two animals were worked with—a pure white rat and a grey Belgian hare. Both were about half grown at the beginning of the experiment. *Red* was the positive color. Food was given with *red* but denied with *green.* No punishment was introduced. The animals were fed for several days in the food box before the stimulus lights were admitted.

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[1] Yerkes and Watson. *The Behavior Monographs.* 1911, vol. 1, no. 2.

Training experiments upon the rat and the rabbit began January 27th. Nineteen days from the beginning of training the animals reached a high percentage of accuracy and thereafter never made more than one or two errors in a normal series. The number of trials per day was 15. Experiments were made daily without interruption for 39 days.

TABLE I

Showing Rise of Red-green Habit

Days	Rat, % correct	Rabbit, % correct
1	50	73
2	53	33
3	53	46
4	66	46
5	73	60
6	73	53
7	73	53
8	80	80
9	60	86
10	53	93
11	73	75
12	73	86
13	73	91
14	53	76
15	66	93
16	53	93
17	86	80
18	66	93
19	86	93
20	86	93
21	86	93
22	93	100
23	93	100
24	100	80
25	93	86
26	93	100
27	93	93
28	100	93
29	100	100
30	93	93
31	93	93
32	93	100
33	100	100
34	100	93
35	86	100
36	86	100
37	100	100
38	93	100
39	100	100
	Considered ready for control series. Total number of trials, 555.	Considered ready for control series. Total number of trials, 555.

While there is nothing wonderful in the formation of this discrimination habit, it does become significant when we contrast it with our failure to get such a habit set up with the *yellow* and *blue* (see page 7). If modern color theories have any phylogenetic reference at all we would expect the formation of the *red-green* habit to be much slower than that of the *yellow-blue*. Taken at their face value the records invite three possibilities of interpretation:—

1st, the animals are discriminating upon the basis of difference in wave length;

2nd, upon the difference in intensity between the two lights;

3rd, only one stimulus is effective (for whatever reason) and no real discrimination is involved. It is possible that the *red* chosen lies outside the spectrum of one or both animals. On this hypothesis the habit might be formed easily. Yerkes,[1] Washburn,[2] Hess,[3] and Watson,[4] have all remarked upon the apparent low stimulating power of *red* light. Another fact which must be taken into consideration in connection with the two stimuli discrimination method, which may have some bearing upon the present work, is the one discussed by Dr. Clara Jean Weidensall. Her results were reported at the Washington meeting of the American Psychological Association (December, 1911). In her work on the discrimination of two *grays* differing greatly in intensity it was shown that, usually, only one stimulus is effective. In other words it is possible to get apparent discrimination between two stimuli where no real discrimination is involved. A further discussion of this point will be given upon page 6.

These three possibilities of interpretation were not clearly foreseen in the early stages of the experiments. Two things lead us to a favorable consideration of the view that the *red* lay outside the animals' spectrum. (1) The fact that, in the control experiments (to be cited below), the complete elimination of *red* failed to change the responses of the animals, and

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[1] Yerkes, Robert M. The Dancing Mouse, New York, 1907.

[2] Washburn, M. F. and Abbott, E. Experiments on the Brightness Value of Red for the Light Adapted Eye of the Rabbit. *Jour. Animal Behavior.* 1912, vol. 2, pp. 145-180.

[3] Hess, C. Experimentelle Untersuchungen zur vergleichenden Physiologie des Gesichtssinnes. *Arch. f. d. ges. Physiol.* 1911, Bd. 142, S. 405-446.

[4] Watson, J. B. Some Experiments Bearing Upon Color Vision in Monkeys. *Jour. Comp. Neurol. and Psychol.* 1909, 1, vol. 19, pp. 1-28.

(2), as will appear in Experiment II, the failure to get discrimination at all between *yellow* and *blue* under similar circumstances. In other words if both colors used in Experiment I had possessed stimulating value, no habit would have been formed under the conditions there obtaining.

Since at the completion of the above set of tests we had no suspicion that the *red* was not stimulating the animals, we began control experiments which were designed to show whether the animals were responding to the difference in wave length or to the difference in intensity. We had planned a rather wide series of tests. We had intended to leave the *red* at full intensity and then gradually to lessen the intensity of the *green* with the rotating sector, and then to repeat the procedure, allowing *green* to remain at the standard intensity. It was hoped either to establish the fact that the habit would maintain itself regardless of the intensity factor, or that at some point where the intensities were equal for the animal, the habit would break down. A few preliminary tests were taken with such astonishing results that we had completely to re-envisage the problem. We cite a few of the experiments:—

1911.

March 7th. *Red* full intensity. *Green* cut to 11% of full intensity. 15 trials. 93% correct.

March 8th. *Green* full intensity. *Red* cut to 11% of full intensity. 15 trials. 100% correct.

March 9th. *Red* full intensity. *Green* cut to 2.7% of full intensity. 11 trials. 40% correct. Complete loss of discrimination. Then immediately afterwards 9 trials were given with both stimuli at full intensity. 100% of correct choices.

March 10th. Conditions as beginning of test on previous day. 15 trials. 53% correct. Complete loss of discrimination. 5 trials were then given with both stimuli at full intensity. 100% correct.

March 11th. Normal series. 15 trials. 100% correct.

From March 11th to May 16th certain experiments were tried to determine the effect of external illumination upon the discrimination. These experiments were so unsatisfactory that mention of the results is omitted. By June 5th the animals were again trained to discriminate perfectly between *red* and *green.* Further control experiments to determine the nature of the effective stimulus were then undertaken.

June 5th. Eight normal trials were first given. 100% correct. Then *red* beam was cut out; *green* left at full intensity. Went to *red side* (darkness) on every trial (10 trials).

June 6th. Eight normal trials. 100% correct. Then *green* was cut out and *red* left at full intensity. *Right position habit developed immediately.* Discrimination lost. Then 4 normal trials were given. 100% correct.

June 7th. Eight normal trials. 100% correct. *Green* out, *red* at full intensity. 14 trials given. *Right position habit developed immediately.* 4 normal trials were then given. 100% correct.

June 10th. Eight normal trials given. 100% correct. *Red* cut out; *green* full intensity. Went to *red side* (darkness) on all 15 trials. 2 normal trials were next given. Both correct.

June 11th. Six normal trials given. 100% correct. *Green* out; *red* full intensity. *Left position habit developed immediately.* (9 trials.) Then 10 normal trials were given. 90% correct.

June 12th. Six normal trials given. 100% correct. *Both* lights cut out for 15 trials. *Right position habit developed.* 4 normal trials were given. 100% correct.[5]

The detailed experiments upon the rabbit are not given. They are identical in character and number with those given the rat. The results are exactly the same except that in the case of the rabbit a decrease of 50% in intensity of the *green* produced disturbance. The work of Washburn and Abbott on the rabbit, showing the lack of stimulation by *red*, had not appeared when our work was completed. Our results are in complete harmony with respect to *red*.

These results seem to show perfectly that the green was the effective stimulus and that the *red* had no stimulating value whatsoever. *The animals were avoiding a lighted compartment.* One might decrease the intensity of the *green* light enormously and eliminate the *red* altogether without changing the accuracy of the responses. When, however, the intensity of the *green* approaches the threshold, as on March 9th, a disturbance immediately manifests itself. Whenever the *green* was cut out the animal behaved exactly as though no light stimulus was present (contrast tests on June 11th with those on June 12th). These results seem to show that we are dealing here with a defect in the receptor rather than with the lack of "attention" cited in Dr. Weidensall's report.

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[5] In all of the control experiments food might be had regardless of stimulus light reacted to. Food was always kept in both compartments even during the training series.

Summarizing the results of Experiment I we find:

1st, that the *green* was the effective stimulus;

2nd, that the *red* had no stimulating effect,—it probably was not discriminated from total darkness. The results harmonize with the hypothesis that the *red* chosen lay outside of the animal's spectrum. Decisive experiments upon this point now in progress, but carried out under different conditions, will soon be reported upon.

It is clear that Experiment I does not touch the problem of sensitivity to differences in the wave lengths which lie within the animal's spectrum.

EXPERIMENT II

On account of the fact that in Experiment I only one stimulus was effective, which made it impossible to test the problem of differential sensitivity with *red* and *green,* we began in the fall of 1911 to test another group of rodents with *yellow* (λ=5950) and *blue* (λ=4780). The stimulus lights were not equated in energy during the training series but were projected directly upon the plaster surfaces. To the human eye the *yellow* was enormously more intense. Before control experiments began the *yellow* and *blue* were equated in energy. The energy value chosen is given by Pfund in the Yerkes and Watson Monograph, p. 81.

January 9th. We began taking records upon two gray Belgian hares and three rats,—one black and white and two pure white. All of the animals had just reached the age of sexual maturity. We were unfortunate in the case of our rabbits. Not one completed the experiment. All three of the rats continued work throughout the experiment. Experiments upon all five of the animals were begun on January 9th. The training series is given for only four of the animals. The record of only one rabbit is given. We had hoped to carry through all of the tests upon Polly, a rabbit which Professor Washburn kindly gave us; one used in her recent light work. Polly had been used to working in illumination and nothing would induce her to work steadily in darkness. All of the other animals worked perfectly under the conditions of the experiment. The animal which is trained while young to work in a dark room goes about the task in a perfectly normal manner.[6]

The marks of the animals are given as follows:

Rat I. Pure white rat, male: fed with *blue*.
Rat II. Pure white rat, male: fed with *yellow*.
Rat III. Hooded black and white rat, male: fed with *blue*.
Rabbit. Gray Belgian Hare, male: fed with *blue*.

It will be seen that the records are not inter-comparative. The two white rats were working with different positive colors. Rat III, although fed with the same color as Rat I, was a black and white rat and consequently possessed pigmented eyes. These differences are especially noted in order that too great uniformity in records may not be demanded.

Table II shows the records made by each animal. We began with two stimuli, then on the 22nd day changed to one stimulus. On the 38th day we changed back to two stimuli. Punishment was introduced in each case on the day designated.

A careful consideration of these records shows, we think, that the discrimination between *yellow* and *blue* was not perfected during the time limits of the experiment. Had we desired to prolong the work the habit would probably have been formed. The paper of Hoge and Stocking (this Journal, vol. II, p. 43) shows that a habit of responding to one of two white lights, 2 and 16 cp. respectively, can be formed by the rat in about 500-600 trials. Had the difference in intensity been less, a much larger number of trials would probably have been necessary. On the assumption that the animals used in the present experiment were reacting to a difference in intensity, we would expect the habit to be formed after a sufficient number of trials. Unfortunately there are no intensity experiments on the Weber-Fechner law in the cases of rats and rabbits to guide us. Since more than 500 trials were given we assume that the relative

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[6] Indeed our experience during the past two years at Hopkins has given us complete confidence in the dark room work. Any argument advanced concerning the "unnaturalness of the conditions" should be supported by experimental proof before receiving consideration.

TABLE II

Showing Lack of Discrimination When Both Stimuli Are Presented at Full Intensity

Date	Rat I (*Blue*) % correct	Rat II (*Yellow*) % correct	Rat III (*Blue*) % correct	Rabbit (*Blue*) % correct
1	60 (2)	60 (2)	70 (2)	60 (2)
2	60	60	20	50
3	40	70	80	70
4	50	40	60	60
5	50	60	70	60
6	50	60	70	70
7	40	10	90	60
8	50	—	10	50
9	40	10	30	50
10	50	20	40	50
11	60	50	60	60
12	70	—	40	60
13	70	60	20	90
14	60	40	70	50
15	60	50	90	80
16	70	70	30	80
17	30	80	80	50
18	40	30	40	60
19	50	40	50	60
20	57	20	40	60
21	57	20	50	60
22	50 (1)	40 (1)	50 (1)	80 (1)
23	80	60	73	70
24	90	70	90	80
25	60	60	60	90
26	90	60	90	70
27	70	50	100	90
28	60	60	80	80
29	80	30	80	90
30	30	50	100	50
31	90	70	100	70
32	100	70	80	70
33	60	60	90	90
34	100	30 (P)	100	60 (P)
35	80	40	90	80
36	100	10	—	—
37	80	60	100	90
38	80 (2)	60 (2)	90 (2)	80
39	70 (P)	70	30 (P)	80
40	50	80	40	80
41	50	70	80	90
42	70	60	50	100
43	70	60	35	100 (2)
44	70	60	80	90
45	70	80	60	80
46	50	70	80	60
47	60	70	40	60
48	10	100	40	80
49	20	90	40	60

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(1) One stimulus introduced.
(2) Second stimulus introduced.
(P) Punishment introduced.
(–) No record for that day.

intensity difference between the *yellow* and *blue* for the animals was less than that between the 2 cp. light and 16 cp. light used in the Hoge and Stocking work. This would account for the failure of our animals to form the habit on the assumption of brightness difference.

Our reason for not prolonging the tests was that we wished to try the method of training the animals to respond to one stimulus (the positive or food stimulus) and then gradually to introduce the second (the light reacted against). Table III shows the results.

TABLE III

SHOWING RAPID RISE OF HABIT WHEN ONE STIMULUS (POSITIVE) IS PRESENTED[7]

Days	Rat I (*Blue*) % correct	Rat II (*Yellow*) % correct	Rat III (*Blue*) % correct	Rabbit (*Blue*) % correct
1	100	30	80	90
2	80	40	80	100
3	70	80	90	90
4	60	70	100	80
5	50	80	70	70
6	60	90	100	90
7	60	80	90	90
8	100	70	100	80
9	60	60	100	100
10	90	100	100	100
11	100	100	100	100
12	90	100	100	70
13	80	60	90	80
14	100	100	70	80
15	90	100	60	90
16	90	70	90	80
17	100	100	100	80
18	100	100	100	100
19	90	100	100	80
20	100	100	100	90
21	100	100	100	100
22	100	100	100	100
23	100	100	100	80
24	100	100	100	100
25	100	100	100	80
26	60	90	100	100
27	100	90	100	90
28	100	100	100	90
29	100	100	100	90
30	100	90	100	100
31	70	100	100	90
32	100	90	100	100
33	100	100	100	70

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[7] It will be remembered that all of these animals had previously worked with one stimulus for about 200 trials (see table II).

All the animals being sufficiently automatic in their responses to one stimulus. we decided gradually to *introduce* the second stimulus. Accordingly both lights were equated in energy. Then the light reacted against was cut down by means of the rotating sector. Table IV shows the results.

In the case of Rat I and the Rabbit (reacting positively to *blue*) the introduction of the second stimulus at the energy designated produced no break down in the habit. The association was maintained fairly well up to the point of equal energy. Rat III (black and white, reacting positively to *blue*) shows extreme unsteadiness for a time after the energy of the *yellow* had been increased to one-tenth that of the blue. This may be due to the fact that the *yellow* possesses slightly more stimulating value for him than for the white rats and the rabbit. Consequently the introduction of the *yellow* (although graduated to the same energy values as for the other animals) was for him more abrupt than for them. The records show that after one or two break downs this animal became very steady. The failure of Rat II to discriminate shows, we think, even without further control tests, that *yellow* has very low stimulating value. Since he was habituated to respond to an intensity value which for him did not lie very high in the scale he was disturbed by the *blue* the moment its intensity equaled that of *yellow*, This point is reached when the energy of the *blue* is one-eighteenth that of *yellow*. All of our tests are in harmony with the view that *blue* has a tremendously high stimulating value.

After Rats I and II had learned to discriminate between the lights at equal energies, control tests were introduced for the purpose of finding out whether the discrimination could be held, whatever the energy relations between the two stimuli. On account of the approach of summer, when the tests were to be discontinued we did not gradually cut down intensity of light *reacted against* as we had previously planned. Instead we chose a variety of tests which we thought would show most rapidly whether the animals were responding to wave length difference or to intensity difference. We give an individual diary record of tests on Rat I. The results of tests on Rat III are quite similar to those reported for Rat I.

TABLE IV

Showing Effect on Habit of Leaving Positive Color at Full Intensity and Gradually Introducing Color Reacted Against

Rat I
(Reacting positively to *blue*)

Days	Angular opening on *yellow*	% correct
1	10	90
2	10	83
3	10	93
4	20	93
5	30	100
6	40	93
7	50	100
8	60	93
9	70	90
10	80	95
11	90	100
12	100	100
13	110	85
14	110	100
15	120	100
16	130	93
17	140	93
18	180	93
19	200	93
20	200	100
21	240	93
22	360 (*)	96
23	360 (*)	100

This shows almost perfect discrimination at equal energy.

Rat II
(Reacting positively to *yellow*)

Days	Angular opening on *blue*	% correct
1	10	80
2	10	80
3	10	80
4	10	90
5	20	80
6	20	75
7	20	90
8	30	80
9	30	77
10	30	50
11	30	60
12	— (1)	94
13	10	100
14	20	80
15	20	75
16	20	80
17	20	60
18		
19		
21		

Could not be brought to full intensity. Shows that animal was reacting to brightness and that *blue* at 20-30° was as bright as the *yellow* at full intensity.

Rat III
(Reacting positively to *blue*)

1	10	100
2	20	86
3	20	86
4	20	100
5	30	85
6	30	33
7	— (1)	80
8	30	40
9	— (1)	100
10	10	75
11	10	60
12	10	95
13	20	100
14	30	75
15	30	85
16	30	95
17	40	93
18	50	100
19	60	100
20	80	80
21	80	83
22	80	85
23	100	100
24	140	100
25	360 (*)	96

Perfect discrimination at full intensity.

Rabbit
(Reacting positively to *blue*)

1	10	70
2	10	83
3	10	100
4	20	80
5	20	90
6	30	93
7	40	80
8	40	90
9	50	90
10	60	85
11	60	95
12	70	95
13	80	90
14	90	93
15	100	94
16	110	85
17	110	93
18	120	93
19	140	85
20	140	93
21	150	86
22	180	90
23	220	85
24	220	93
25	360 (*)	80

Animal died. Was discriminating fairly well at equal energy. Death was due to cancerous growth upon neck; during the past month growth had increased enormously in size. Animal worked faithfully until the day before his death.

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(1) Only one stimulus used for that day.
(*) Equal energy.

Control tests on Rat I (reacting positively to *blue*)

May 3rd. After normal series at equal energies[8] *blue* was cut to 20° opening. Animal set up *right position* habit. Discrimination lost. Normal series (5 trials) given again. Animal went to *blue* as usual. The behavior of Rat II (*yellow*) had prepared us for this type of result. The *blue* to them is high in the scale of intensity; the *yellow* very low. When the *blue* was brought down to one-eighteenth the energy of the *yellow*, the two stimuli were too nearly equal in intensity to afford a basis for a differential response. It may be argued that we had reduced the intensity of the *blue* below the animal's threshold. A long series of experiments shows that the *blue* still stimulates the animals when the angular opening is between 1 and 2 degrees. The *yellow* threshold, on the other hand, lies much higher. Our reason for not reporting upon this is due to the fact that we have made the threshold tests throughout the spectrum a separate study. It may be safely taken for granted that the threshold for *blue* is below a 5° opening, whereas that for *yellow* is probably not much below 10°[9] (lower, somewhat, for the black and white rat than for the white).

May 4th. Normal series of 10 trials, all correct, *blue* cut out. Animal was frightened at first (the change in condition for him must have been large) and would hardly respond at all. First trial went to *blue* side (darkness); then went to *yellow* (light side) on every trial for 9 trials. Equal energy series of 5 trials then given. Went to *blue* on every trial.

May 5th. Normal series, equal energies, 10 trials, 100% correct. Then *blue* was cut to 10°, *yellow* full intensity. 7 trials. Animal fell back on position habit. Went to right on every trial. Then *blue* was cut out for 10 trials. Went to *yellow* on every trial. Next *blue* was cut to 10°. 6 trials. Went to *yellow* on every trial.

May 6th. *Yellow* full intensity, *blue* cut to 10°. 10 trials given. Went to *yellow* on every trial.

The test upon these two days with 10° opening upon *blue* show that we are working with the stimuli at the point where they possess approximately equal stimulating power. We get one of two reactions without being able to predict which will occur, *viz.*, a break down in habit or a complete reversal with respect to choice of light. Possibly our inability to predict the response may be due to slight fluctuations in the current supplying the arc, which would alter the intensity of the two lights unequally (the distribution of energy in the spectrum of any source varies greatly, depending upon the temperature at which the source is burned).

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[8] By normal series, we mean in all cases about ten trials with both stimuli at equal energy (unless otherwise stated).

[9] In most places in this paper the angular opening is given. This is for the convenience of anyone desiring to repeat the work. If the relation in terms of energy is desired, it will be remembered that the work of Brodhun and of Hyde abundantly proves the Talbot-Plateau law.

Similar tests upon Rat II (reacting positively to *yellow*)

Table IV shows that this animal never learned to discriminate between the *yellow* and *blue* at anything like equal energies. This gave us an opportunity to test the question of reversal in choice of positive light. The tests show without discussion that his discrimination had been based upon the difference in intensity.

April 26th. Gave series of 15 trials with *yellow* as only stimulus, 93% correct. This was done to bring animal back to normal habit of reacting to one stimulus. Then for 7 trials full intensity *blue* was substituted for the *yellow. Went to blue on every trial.*

April 27th. Yellow and *blue* full intensity, 10 trials. *Chose blue on every test.* Then *blue* was cut out and *yellow* given alone. 10 trials, 80% correct.

April 30th. Yellow alone, full intensity, 15 trials, 100% correct.

May 1st. Yellow and *blue* full intensity, 20 trials. *Went to blue on every trial.* This shows the same results as tests on April 27th.

Another series of tests was undertaken where *white* light (from Nernst filament projected direct upon plaster surface) was substituted for *blue* or *yellow* at will.[10]

May 16th. Yellow (animal's positive color) at full intensity. Nernst in place of *blue.* 9 trials. Animal went to *white* light on every trial. Immediately following this test one was given in which *white* light was substituted for *yellow.* 10 trials. Went to *white* light on every trial.

May 17th. Another series was given with identical results.

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[10] It will be remembered that Washburn suggested this type of test at the Boston meeting of the American Psychological Association (1910).

CONCLUSIONS

1. The evidence seems to justify the conclusion that the long wave lengths stimulate the visual receptors of the rodents very slightly or not at all. Where their spectrum begins at the red end cannot be decided by the above type of experimentation.

2. Experiment II offers good but not absolutely conclusive evidence that the rats can respond only to difference in intensity of monochromatic light. On account of the low stimulating value of *red* and *yellow* our choice of stimuli was not very good. *Blue* and *green* would have been better. To the adherents of color theories the denial of a response based upon wave length, both in the case of *red* and *green* and of *yellow* and *blue* is the equivalent of denying the possibility of a response on the basis of wave length anywhere in the animal's spectrum. If the data on *blue* and *green* were at hand and spoke as clearly for intensity difference, we believe that we could say with some certainty that wave length is not a factor in the visual responses of rodents.

A PRACTICAL DEVICE TO SIMULATE THE WORKING OF NERVOUS DISCHARGES

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First we shall briefly outline a theory which will reconcile observed facts as to the structure of nervous systems and the reactions of such systems. We will then take up the description of a practical mechanical contrivance which will represent the essential elements of a nervous system and which will react in the same way. We will then compare the results obtained with the machine with those given by live nervous connections. In this discussion we shall confine our field to the interactions of the nerves. What happens in sensory endings like those of smell and taste does not concern us. The reader should also avoid thinking of what he knows of his own sensations and have in mind only what he can observe in the nervous systems of other creatures.

A nervous system may be taken as controlling several pairs of opposing muscles through a system of nervous channels excited by a number of sensory terminals. A muscular movement or response is caused by a combination of discharges from several channels acting on a given muscle or muscles more than on the muscle or muscles directly opposed to it or them. The said combination of discharges may be excited at one or several sensory points.

As a result of individual experience changes take place in the nervous channels. With the same sensations[1] as before we observe that the responses have changed and vice versa we observe the same responses when the sensations have changed. The most natural explanation for this is that some of the channels have grown more than others, that is, that they have become more open to the flux.

The problem that is before us is to account for the growth of certain channels more than others. Take the familiar but perplexing case of inhibition of muscular action shown here by diagram. (Figure 001.) Let S1 and S2 be sensations. M1 represents a forward movement, M2 a backward movement. S1, M1 and S2, M2 are channels of good conductivity. The cross channel S1, x, M2 is of low conductivity so that before experience is gotten, sensation S1 gives response M1 a forward movement. After experience is had we observe the sensation S1 is followed by response M2, a backward movement. We conclude that channel S1, x, M2 has as a result of experience become of high conductivity, exceeding S1, M1. How can we explain this? How can experience have developed the weak channel and not the strong one?

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[1] Throughout this article the term *sensation* is used to represent the excitement of a sensory terminal of a nervous channel. Of course this departure from the usual subjective meaning of the word is made for the sake of brevity.

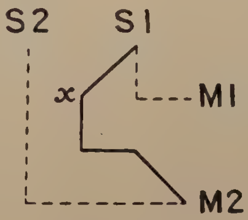

FIGURE 001

Now, as to the conductivity of nerves we find evidence to support the following premises:

1. The effect at the motor end of a nervous channel is not always in proportion to the intensity of the impression at the sensory end. We may state it thus: The susceptibility of a nervous channel is greater at one time than at another or conversely we may state: The resistance of a channel to nervous discharges is less at one time than at another. The same rule will hold it is believed even though the nerves forming the channel considered be perfectly normal as to nourishment; that is to say that normally nourished nerves are of variable susceptibility.

2. The first discharge through a channel after a period of rest will increase the susceptibility. If the impression at the sensory end is repeated at proper short intervals the susceptibility will be steadily increased.[2]

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[2] Spencer, Herbert. Principles of Psychology. New York, 1894, pp. 577, 614. Thorndike, E. L. Animal Intelligence. New York, 1911, p. 267.

3. If the impressions are followed by a period of rest, the longer the rest the greater will be the decrease found in the susceptibility. That is to say the susceptibility of a channel decreases with disuse.[3]

4. There is, however, a permanent increase in the susceptibility of a nervous channel caused by repeated discharges.

5. If a given channel has several sensory endings S1, S2, S3 and one or more motor endings M, a discharge from S1 to M will increase the susceptibility to a discharge from S2 or S3 to M. Hence if S1 and S2 are excited in succession there will be a temporary increase in the susceptibility of the channel and also a permanent growth.[4]

6. When several channels are open to a nervous discharge, the discharge will be divided among the channels in proportion to the susceptibility at the time.

In order to save space no attempt will here be made to prove the reasonableness of the above premises. It is proper to say, however, that in the main they are in accord with the statements of writers of authority as will be found on consulting well known works on the subject.[5]

It may help some thinkers to form a clear idea of the effect of the time interval between discharges upon the susceptibility of the channel if we present it in the shape of a formula:

Let
CT = Combined present capacity of all channels
C1 = Present capacity of the given channel
CP = Original capacity of the given channel plus the permanent increase made by previous discharges.
CL = Temporary additional capacity of the given channel at the last discharge
t = Time since the last discharge through the given channel

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[3] Thorndike, E. L. Animal Intelligence. New York, 1911, pp. 44, 249.
Meyer, Max. Fundamental Laws of Human Behavior. Boston, 1911, p. 86.

[4] Meyer, Max. Fundamental Laws of Human Behavior. Boston, 1911, p. 129.

[5] Special reference should here be made to the recently published book of Professor Meyer, Fundamental Laws of Human Behavior, for the reason that his argument is not altogether unlike that of this article. The writer will not presume to pass judgment on the book further than to say that in spite of its illuminating and most suggestive exposition it leaves room for further elucidation of the matter in hand.

e = Unknown exponent
a & b = Unknown constants
$F1$ = Discharge through the given channel
FT = Discharge through all channels

Our present capacity is then from premises 2, 3 and 4

$$C1 = CP + CL + a - bt^e$$

and from premise 6 we have

$$\frac{F1}{FT} = \frac{C1}{CT}$$

Having now a conception of how the susceptibility of a nervous channel will increase with each discharge and decrease with disuse, let us take up the problem of inhibition again. We will now modify our diagram so as to give this (Figure 002):

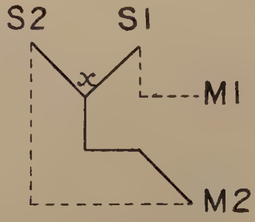

FIGURE 002

As before, S1, M1 and S2, M2 are channels of good conductivity. The median channel S1, S2, x, M2 is one originally of low conductivity. Now let the environment be such that the movement M1 habitually produces the sensation S2.

From our premises we see that at each experience the susceptibility of channel S1, S2, x, M2 is increased because its first discharge is followed quickly by a second. It is evident that the median channel will, after repeated experiences, become of high conductivity so that eventually the sensation S1 will be followed either by movement M2 or at least by a prevention of M1 which is inhibition, as the movements are opposed.

We now see how experience can develop the weak channel faster than the strong one. This case may be considered as one of converging nervous channels.

To illustrate the case: the sight of the fire excites a forward movement, M1. The sharp pain of the burn excites a backward movement, M2. After repeated experiences the sight of the fire no longer excites a forward movement.

Let us now pass to the problem of association of ideas. The diagram given here will illustrate it (Figure 003). Ma and Mb represent movements not opposed to each other.

As before, the channels Sa, Ma and Sb, Mb are of high conductivity while the median channel Sa, Sb, x, y, Ma, Mb is originally of low conductivity so that before experience the sensation Sa is followed only by the movement Ma and the sensation Sb is followed only by the movement Mb. Now let the environment be such that the sensation Sa is always succeeded quickly by Sb or vice versa. The discharge through the median channel Sa, Sb, x, y, Ma, Mb will be greater at each experience from our premises as in inhibition so that after a number of experiences the sensation Sa (or Sb) will result in both movements Ma and Mb. Again the weak channel has grown faster and overtaken the strong ones. Eventually the originally weak channel will have dwarfed the others and for either sensation the discharge will be practically equal at Ma and Mb.

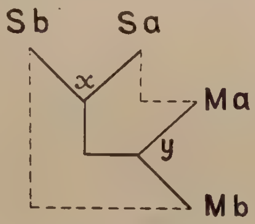

FIGURE 003

This case we may call one of diverging nervous channels. In it may be found the physiological accompaniment of the association of ideas.

As an illustration: the crack of the whip (Sa) makes the young horse prick up his ears (Ma); the sting of a blow makes him jump forward (Mb). If the blow often follows the sound, the jump will after a while be excited by cracking the whip. The ideas of the sound and the pain have become associated as the psychologist would say.

Looking at the problem from a quite different point of view for a moment, we may picture our nervous channels as chains or groups of neurons, each neuron being an individual organism.

A group of neurons may be likened to a colony of animals having points of contact with each other. Each neuron will resemble a wriggling animal with arms like an octopus. If any one animal is disturbed and made to wriggle, its movements are communicated to the adjoining animals which are disturbed and wriggle in turn. When the external disturbance ceases the animals gradually come to rest, then as gradually sink into sleep. The more often a given animal is irritated the more irritable he becomes. Disturbances will be conveyed through a colony on certain lines determined by experience. In a similar manner are disturbances transmitted through a nervous system.

Having given the above brief outline of a theory for the working of nervous discharges, a few words as to its significance may not be amiss. Present day explanations of the working of nervous discharges are so inadequate that they are helpful to few. They leave large gaps to be filled by the imagination.

A clear understanding of the working of the nervous system that would reach the great body of world students and be as lucid as the modern demonstration of the circulation of the blood would be a great acquisition to the cause of general education.

That such a clear understanding will some day be reached is most probable. It must be approached step by step. The step aimed at here is the first that naturally presents itself, for we find that a simple nervous discharge following a well defined channel as in simple reflex action, presents no difficulty to the scientific mind. The first step is then to explain such operations as learning, inhibition and habit forming. If we can make these clear to interested minds a barrier will be passed. That there will be other barriers to cross before animal intelligence is fully understood goes without saying.

The significance and importance of a proper solution of the problem can not be better stated than in the words of that high authority, Dr. Loeb,[6] viz.:

"The unravelling of the mechanism of associative memory is the great discovery to be made in the field of brain physiology and psychology."

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[6] Loeb, J. Comparative Physiology of the Brain and Comparative Psychology. New York and London, 1900, p. 14.

The working of nervous systems has been viewed by science mainly in two aspects. First, the physiologists have studied their structure, growth and functions by dissection and experiment. Secondly, experimenters in the laws of animal behavior have gathered data of value from scientific observation. Under the same head might be put facts generally known about the training of animals and the teaching of young children. Our knowledge of the effect of time and of repetition in modifying nervous action is derived mainly from the sources under the second head.

It is thought that the engineering profession has not contributed greatly to the study of nervous systems, at least since Herbert Spencer, an engineer, wrote his book on psychology. As the co-operation of workers in different fields of knowledge is necessary in these days of specialists it may be argued that engineers can consistently join in the consideration of a subject of such importance to man. As a member of the engineering profession then, the writer is not without excuse for advancing ideas on the working of nervous systems for the consideration of physiologists and others who have knowledge of the matter.

In discussing the subject of this article diagrams are necessary and demand no apology. To many minds the explanation here given of the modification through sensory experience of nervous channels may be clear enough and even sufficiently convincing. It is thought, however, that the hypotheses advanced could be made more convincing to others if they were embodied in a practical mechanical device such as could be built and operated. This device would simulate the working of nervous discharges by purely mechanical means. With it, one could demonstrate the modification of action or behavior by experience.

OPERATION

Figures 1, 2, and 3 show the construction to be used with compressed air or hydraulic pressure. In this description it will be assumed that hydraulic pressure is used.

In figure 1 the slide valve 6 is shown at the extreme end of its inward stroke as in receiving a signal. This valve, known as the spur valve, when in this position, opens ports 4 and 5 on the pressure side. The spur valve spring 7 is now compressed. The pawl 8 which is attached to the spur valve, is

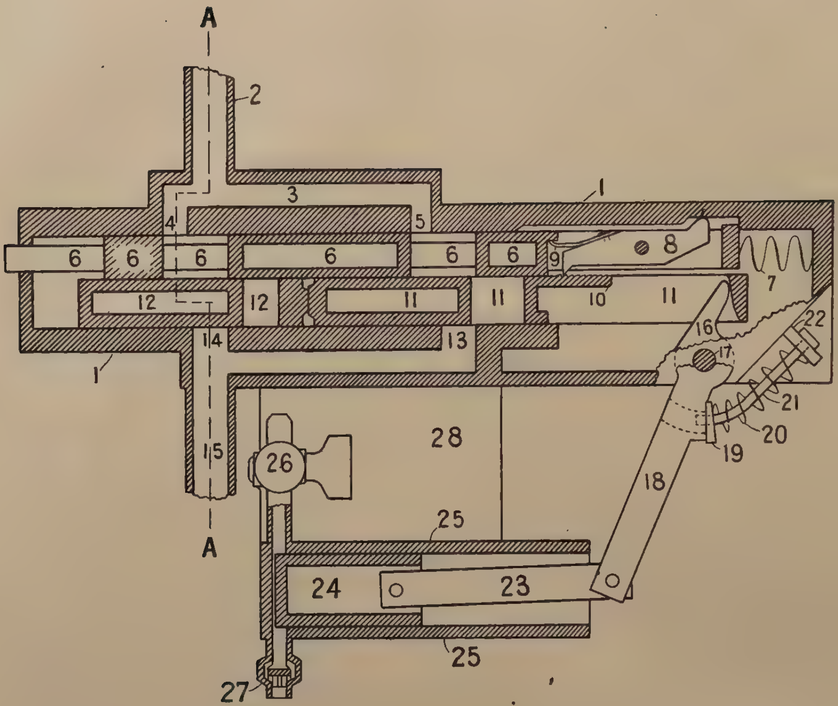


FIGURE 1. Transmitter. Longitudinal section on line B B of Figure 2

REFERENCE NUMBERS

FIGURES 1-4

1 Transmitter case
2 Pressure pipe
3, 4 and 5, Pressure ports
6 Spur valve
7 Spur valve spring
8 Pawl
9 Pawl spring
10 Ratchet
11 Ratchet valve
12 Lag valve
13, 14 Issue ports
15 Meter pipe
16 Rocking finger
17 Finger shaft
18 Finger lever
19 Washer
20 Lever spring
21 Guide pin
22 Spring lug
23 Connecting rod
24 Plunger (dash pot)
25 Dash pot barrel
26 Adjusting cock
27 Check valve (dash pot)
28 Bracket (dash pot)
29 Main pressure pipe
30, 31 Collecting pipes
32, 33 Meter cones
34, 35 Meter discs
36, 37 Guides
38 Meter stem
39 Meter link
40 Rocking lever
41 Connecting rod
42 Slide valve rod
43 Balanced slide valve
44 Valve chamber
45 Cylinder
46 Piston
47 Piston rod
48 Cylinder barrel
49 Exhaust port
M1 and M2 Admission ports
50 and 52 Exhaust passage
51 Pressure pipe
53 Exhaust outlet
S1n, S3n, S5n, S2n, etc. Transmitters
115, 116 Key Rods (S1 and S2)
117, 118, 119 Spur rods
120, 121 Bell cranks
122 Suspender links
123 Coupling gang frame

held down on ratchet 10 by the pawl spring 9 so as to engage it. Valve 6 slides over the lag valve 12 and the ratchet valve 11.

The ratchet valve 11 is shown in the figure in its original position or right hand end of its stroke. When valve 6 is permitted to make its return or outward stroke the valve 11 moves also, pushed by the pawl 8. If valve 6 has a stroke of one and one-half inches, valve 11 will move with it about one-fourth inch. The lag valve 12 will also move the same distance pushed by valve 11. When one-fourth inch of the return stroke has been made, pawl 8 is tripped by the striking of the lug on top of the pawl against a shoulder in casing 1. When the ratchet valve is thus released, it moves to the right, driven by lever spring 20 acting through finger lever 18, finger shaft 17 and rocking finger 16. When ratchet valve 11 moves to left it acts through the said finger lever, etc., together with connecting rod 23 so as to draw out dash pot plunger 24 and thus suck air (or water) through check valve 27. When, on the other hand the ratchet valve moves to the right, the dash pot plunger is driven back by the action of lever spring 20. The air now contained in dash pot 25 is prevented from escaping by check valve 27 and can only pass out through adjusting cock 26. In this way the return stroke of ratchet valve is retarded and is very slow. When ratchet valve moves to right on its return stroke it leaves the lag valve 12 behind.

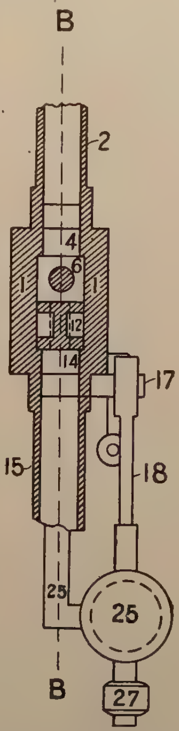


Figure 2. Transmitter. Transverse section on line A A of Figure 1.

If the time interval before a second stroke of spur valve 6 is long enough, ratchet valve 11 will have reached its original position and its second stroke will be the same as the first and lag valve 12 will not be moved. If on the other hand, the time interval is short so that the second stroke of the spur valve comes before the ratchet valve has arrived at its original position, the ratchet will cause the ratchet valve to advance further to the left than before and hence the lag valve will be advanced further to the left.

Now, the further valve 11 moves to the left the greater will be the effective opening for water from pressure port 5 to issue port 13. Hence the effective opening at any stroke will be in inverse proportion to the time interval since the previous stroke. In other words the passage way will gradually close between strokes.

In the case of the lag valve 12, the further it moves to the left the greater will be the effective opening for water from pressure port 4 to issue port 14. As this valve always moves to the left, it will be seen that the effective opening through valve 12 is proportional to the maximum previous opening of the ratchet valve.

The combined effective area of valves 11 and 12 gives the effective area of the transmitter, and it will be seen that this area is susceptible to increase two ways, viz., temporary increase by valve 11 and permanent increase by valve 12. A rapid succession of strokes of the spur valve will cause a decided increase of opening through the transmitter and hence a decided increase in the discharge through the same when open. The hydraulic pressure in pressure pipe 2 is assumed to remain constant.

It will be noted that when the spur valve is in its outward position all ports are closed and there is no discharge through the transmitter. When the spur valve is moved inward, however, it creates an opening the effective area of which depends on the position at the time of the ratchet and lag valves.

In other words, the transmitter is a valve whose maximum opening is variable and is determined by the frequency of operating. Between operations the maximum opening is automatically and gradually reduced.

In figure 3 several transmitters, S1n, S3n, etc., are shown connected so that their meter pipes 15 enter into a manifold pipe 31. There are also several transmitters, S2n, S4n, etc., similarly connected into a manifold pipe 30. In the figure the transmitters are shown in a horizontal line for the sake of simplicity. Of course, they will work just as well if arranged in vertical columns with proper connections. Collecting pipes 30 and 31 discharge into opposite sides of exhaust passage 52 through meter cones 32 and 33. The discharge from 31 through 33 impinges on meter disc 35 tending to move it to the right

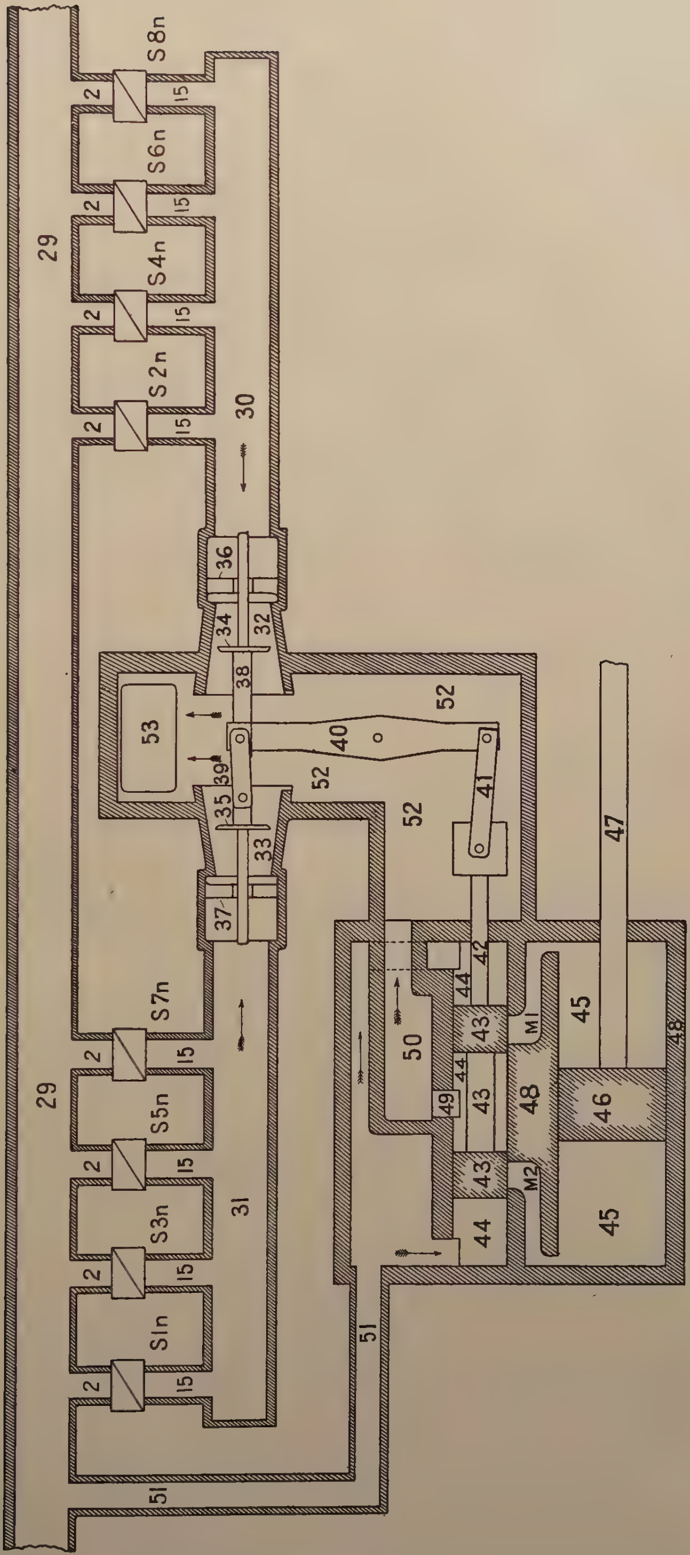


FIGURE 3. Stream meter, slide valve and cylinder. Longitudinal section.

while the discharge through 32 tends similarly to move meter disc 34 to the left. These discs are mounted on meter stem 38 which moves in guides 36 and 37. In figure 3 the meter stem is shown in mid position as it would be if the discharges from 30 and 31 were equal. Should the stream from pipe 30 become greater than the other the discs would take a position more to the left.

The position of the meter discs determines the position of slide valve 43 through the meter link 39, the rocking lever 40, the connecting rod 41 and the slide valve rod 42. The slide valve should be balanced so as to reduce friction. When it moves to the right it opens admission port M2 to pressure from pipe 51 through chamber 44 and it opens port M1 to exhaust passage 50 through 44 thus causing the piston 46 to move to the right. The slide valve ports, piston, etc., are of familiar construction.

The combination of discs, cones, etc., forms the *stream meter*. It will be seen that the stream meter controls the hydraulic cylinder. But the stream meter is controlled in turn by the transmitters that govern the tributary streams. If the sum of the streams from transmitters S2n, S4n, S6n, and S8n, be greater than the sum of the streams from transmitters S1n, S3n, S5n, and S7n, the piston rod 47 will move out. If it be less, the piston rod will move in. Now, the stream from a single transmitter is variable as has been shown, so that the stream from S2n alone may be greater than the added streams from S1n and S3n. From this it may be seen that if the transmitters S1n, S3n, and S2n are opened simultaneously, the movement of the piston rod may be either outward or inward according to the frequency with which S2n has previously been operated.

By the system above described we see that we have a hydraulic cylinder that is subject to the control of any one of its transmitters and also to a variety of combinations of transmitters working in concert, the result in each case depending largely upon what might be called the "experience" of the transmitters in the combination.

The system described is for use with hydraulic pressure or compressed air. An equally practical system which will not here be described is for use with electric control, i.e., with electric transmitters and with electro magnets controlling the slide valve of the hydraulic cylinder.

Figure 4 shows the construction of a *coupling gang* which is an appliance for working groups of transmitters in combination. In this particular coupling gang there are 5 transmitters operated by two key rods. Each key rod opens 3 transmitters. When a key rod is moved downward the motion is communicated through the connecting bell-cranks to the spur rods which move horizontally. Spur rod 19 for transmitter S6n is moved by either key rod by means of slotted holes for the bell-crank pins. Each spur rod pushes against and works the spur valve of a transmitter.

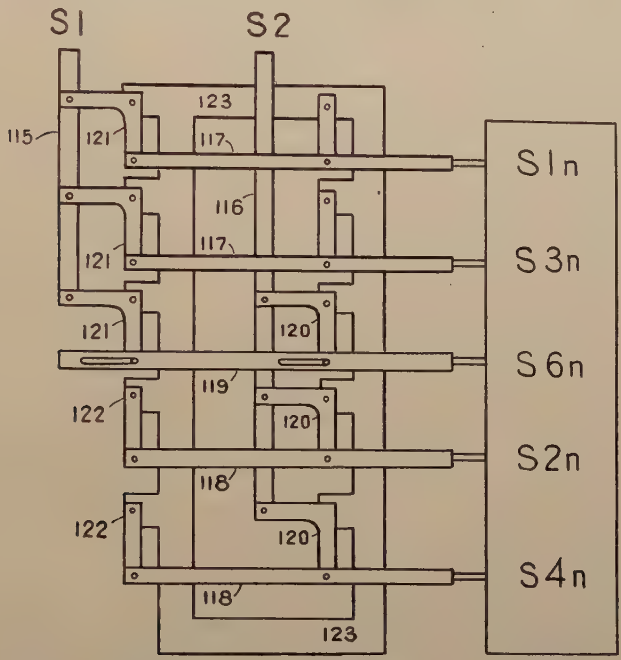
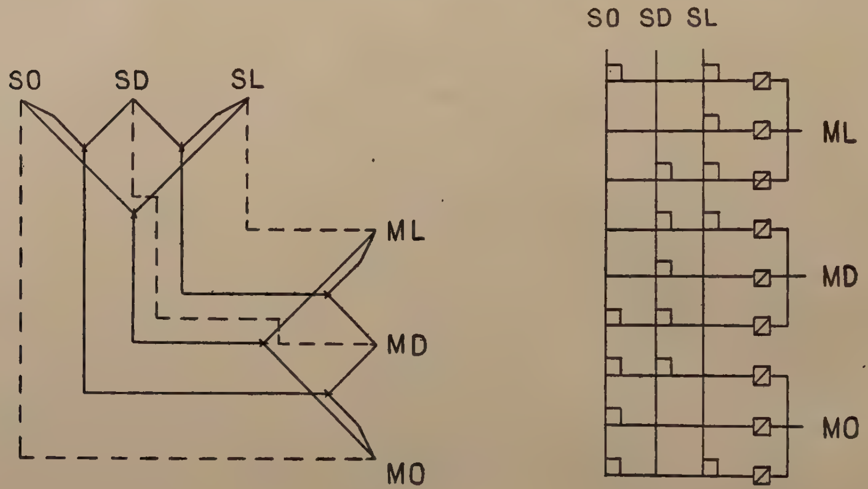


FIGURE 4. Side view of a coupling gang for 5 transmitters.

It is evident that a coupling gang on this order may be used to control all the transmitters of a given stream meter. Or a coupling gang may be used to co-ordinate the movements of several hydraulic cylinders through their respective transmitters and stream meters.

To show how different forms of coupling gangs may be employed, diagrams of two arrangements are shown in figures 5 and 6 and tables are used for others. In figure 5 the left hand diagram FL known as a stream diagram shows diagrammatically the form of the hypothetical channels that connect the sensory terminals SO, SD and SL at the top of the diagram with the motor terminals MO, MD and ML at the right of the diagram. The broken lines show the direct channels that prevail at first. The solid lines show the channels that are developed by favorable experience. Figure 6 shows a similar stream diagram referred to again later.



FL. FR.

Figure 5. Coupling diagram and stream diagram for a 3-way diverging gang of 9 transmitters.

In figure 5 the right hand diagram FR, known as a coupling diagram, shows how the key and spur rods are arranged and connected so as to work the transmitters. The key rods are represented by vertical lines and the spur rods are shown by horizontal lines. The bell crank connections to be used are indicated. A single transmitter connected to one key rod corresponds to a direct channel. Two transmitters connected to the same two key rods correspond to a diverging channel. Each transmitter is indicated by a square with diagonal line. The pipe lines connecting the transmitters into groups are indicated by connecting lines on the right. Each group of connected transmitters will act as one, on a certain stream meter controlling a hydraulic cylinder. The meters and cylinders are not shown.

In the case of figure 6 no coupling diagram is given but the arrangement of the rods and connecting bell cranks is adequately shown in tabular form in table III. Each key rod is represented by a column and each spur rod by a row. B.C. at the intersection indicates a bell crank connection. x1, x2 and x3 refer to corresponding connections in figure 6. The motor connections are in the right hand column. Sn in the next column indicates a transmitter. Other forms of coupling gangs are shown by means of tables similar to table III. No stream diagrams are shown for some of these arrangements but one could readily be constructed from each table by aid of figures 002, 003, 5 and 6. We will now take up briefly each form of coupling gang, beginning with the simplest.

In table I is represented a converging gang which may be used like that shown in figure 4 to illustrate the theory for in-

TABLE I (Fig. 002)

CONVERGING GANG

Key Rods			Movement
S 2	S 1		
—	B.C.	S n	M 1
B.C.x	B.C.x	S n	M 2
B.C.	—	S n	"

TABLE II (Fig. 003)

DIVERGING GANG

Key Rods			Movement
S b	S a		
—	B.C.	S n	M a
B.C.	B.C.	S n	"
B.C.	B.C.	S n	M b
B.C	—	S n	"

hibition as explained previously. Table II represents a diverging gang to illustrate the association of ideas as explained.

Figure 5 shows how three movements, MO, MD and ML, may be so co-ordinated that one key rod can, after the required experience, cause three cylinders to move together where originally only one of the cylinders was started by the said rod.

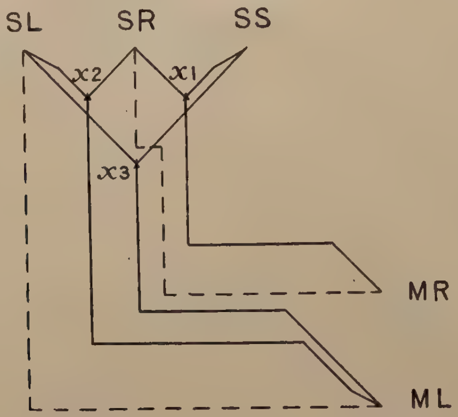


FIGURE 6. Stream diagram for a duplex converging gang.

Figure 6 and table III show a duplex converging gang. In this arrangement the first key rod (or sensory terminal) SS is known as the station key. MR and ML are opposite movements. If SS and SL are habitually struck in succession except when SS, SR and SL are struck in succession the device will become "trained" so that when SS is struck the move-

TABLE III (Fig. 6)

DUPLEX CONVERGING GANG

Key Rods				Movement
S L	S R	S S		
—	B.C.x1	B.C.x1	S n	M R
—	B.C.	—	S n	"
B.C.x2	B.C.x2	—	S n	M L
B.C.x3	—	B.C.x3	S n	"
B.C.	—	—	S n	"

ment ML will result. On the other hand if SS and SR are habitually struck in succession the key SS will when struck give the opposite movement MR.

TABLE IV

6 Way Diverging Gang of 24 Transmitters

Key Rods							Movement
S U	S D	S L	S R	S O	S I		
B.C.	—	—	—	—	B.C.	S n	M I
—	B.C.	—	—	—	B.C.	S n	"
—	—	B.C.	—	—	B.C.	S n	"
—	—	—	B.C.	—	B.C.	S n	"
B.C.	—	—	—	B.C.	—	S n	M O
—	B.C.	—	—	B.C.	—	S n	"
—	—	B.C.	—	B.C.	—	S n	"
—	—	—	B.C.	B.C.	—	S n	"
B.C.	—	—	B.C.	—	—	S n	M R
—	B.C.	—	B.C.	—	—	S n	"
—	—	—	B.C.	B.C.	—	S n	"
—	—	—	B.C.	—	B.C.	S n	"
B.C.	—	B.C.	—	—	—	S n	M L
—	B.C.	B.C.	—	—	—	S n	"
—	—	B.C.	—	B.C.	—	S n	"
—	—	B.C.	—	—	B.C.	S n	"
—	B.C.	B.C.	—	—	—	S n	M D
—	B.C.	—	B.C.	—	—	S n	"
—	B.C.	—	—	B.C.	—	S n	"
—	B.C.	—	—	—	B.C.	S n	"
B.C.	—	B.C.	—	—	—	S n	M U
B.C.	—	—	B.C.	—	—	S n	"
B.C.	—	—	—	B.C.	—	S n	"
B.C.	—	—	—	—	B.C.	S n	"

This arrangement is of special interest, as with it we can simulate the working of nervous discharges in an animal learning the path around an obstacle. The key SS corresponds to the sensation arising from the situation. MR is turning to right. ML is turning to left. The animal after experience turns to the left we will say at the signal SS. The machine after similar experience acts similarly.

In table IV a 6-way diverging gang is shown without any diagram. By this arrangement three hydraulic cylinders may be controlled and thus we could govern movements in three directions as in and out, right and left and up and down. After suitable experience the striking of a single key rod would cause movement in two or three directions, as will be seen by a study of the table, if one remembers that the discharge from a transmitter increases when it is operated at short intervals.

Table V represents a tandem converging gang. S1, M1, and SR1, MR and SR2, MR correspond to channels originally of high conductivity, (first, fourth and fifth rows), while S1, SR1, MR and S1, SR2, MR corresponds to channels originally of low conductivity. Now let the environment be such that the sensation S1 is soon followed by the sensation SR1 and such that the response MR brings about a sensation SR2, it will be seen that the channel S1, SR1, MR and the channel S1, SR2, MR (second and third rows) will grow at each experience and the result will be that the signal S1 will be strongly connected to the response MR or in other words that the transmitters in the second and third rows of the table will give increased discharge.

TABLE V

Tandem Converging Gang

Key Rods				Movement
SR 2	SR 1	S 1		
—	—	B.C.	S n	M 1
—	B.C.	B.C.	S n	M R
B.C.	—	B.C.	S n	“
—	B.C.	—	S n	“
B.C.	—	—	S n	“

This mechanism is of especial interest as it illustrates the physiological accompaniment of a form of satisfaction, showing how associations may be reinforced or stamped in. Such satisfaction we may say is the antithesis of inhibition.

To explain, it is thought that where the situation is such that a given response is followed by a new or changed sensation which gives the same response the effect is a form of satisfaction. To illustrate this, if the puppy is induced to suck the teat and the sucking results in a pleasant taste which causes him to suck harder, that is satisfaction.

The signal SR_2 in table V belongs to a class that may be known as counter signals. A counter signal is a signal (or sensation) that is due to the reaction of the environment to a given motor response. A counter signal may be inhibiting or reinforcing or otherwise according to the structure of the nervous channels (or coupling gang). For example, the whine of the infant is a motor response and its counter signal is the offer of the nipple. The sucking is a motor response and its counter signal is a pleasant taste. S_2, table I, is also a counter signal. Counter signals or sensations play an important part in the development of nervous channels as has been shown for simple cases of inhibition and satisfaction. It is largely through the effect of counter signals on the nervous system that it is brought into proper correspondence with the creature's environment.

It is evident that the forms that we have illustrated in the figures and tables could be combined in various ways so that many types of response to situation could be simulated. For example, the arrangement shown in table V may be modified by adding two more key rods on the left and four more transmitters. By suitable connections we will have a two way tandem converging gang which will simulate the selection of responses by satisfaction. Whatever system of coupling be employed to control a plurality of movements there will be found the same general principle throughout. Along with the description we have incidentally observed how the mechanical action simulated particular nervous developments. As to general analogy of the apparatus with a nervous system we may briefly note:

A 1, A simultaneous flow in several meterpipes results in a certain movement or movements.

A 2, A simultaneous flux in several nerves results similarly in a certain movement or movements.

B, The effect of time intervals between discharges in determining variation of response is the same in the apparatus as it is in a nervous system.

Of course there are types of response to environment that are not covered by this discussion. It is believed, however, that the theory advanced herein with some modifications will be found to answer for a large part of the field which is not included.

In reviewing the different arrangements shown in our tables and diagrams one fact seems to be brought into prominence. It is that the channel that is to be made to govern after suitable experience must be there in the first place as part of the structure. In regard to nervous systems this is not such a great difficulty as it may seem. Remember the shocking stupidity often shown by animals usually thought intelligent and the limited field in which animals can be trained. On the other hand there is reason to think that in life many nervous channels remain undeveloped. Moreover there is abundant evidence in animal behavior to show that the associative memory of each species is in proportion to the complexity of its nervous system.[7]

Our mechanical system may be thought at fault because it requires signals to succeed each other in order to affect the opening of the transmitters, so that if two sensations were simultaneous they would never become associated together. The answer is that each of two simultaneous signals may be associated with a common signal which precedes them.

To summarize briefly the points covered we have shown that a comparatively weak nervous channel may become a comparatively strong one if it be provided with two sensory points and with outside occurrences that shall cause the two points to be excited in succession from time to time. We have shown how this principle will account for the different ways of learning and habit forming.

We have also demonstrated a mechanism that will simulate in its various forms the working of nervous discharges. With it, as in a nervous system, we find that as a result of individual experience, changes take place so that with the same signals as before the responses have changed and vice versa we find the same responses when the signals have changed. We have a mechanism that can be trained, that can acquire habits, that will move either forward or back at a given signal according to experience, that will make one, two or three responses to a given signal according to experience.

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[7] Loeb, J. Comparative Physiology of the Brain and Comparative Psychology. New York and London, 1900, p. 13.

In other words we have shown a practical arrangement of mechanical transmitters and receivers that will respond to signals and control movements like a nervous system and that possesses associative memory as it can learn by experience. For, quoting Dr. Loeb again, "If an animal can be trained, if it can learn, it possesses associative memory."

THE BEHAVIOR OF A PARASITIC COPEPOD, *LERNAEOPODA EDWARDSII* OLSSON

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I. GENERAL REMARKS

The data presented in this paper were obtained during July and August of 1912, while the author was in the service of the Wisconsin Fish Commission, studying an outbreak of parasitic copepods in the trout hatchery at Wild Rose, Wis. The brook trout, *Salvelinus fontinalis,* were found to be attacked by the copepod *Lernaeopoda edwardsii.* Most generally this parasite attaches itself to the filaments of the gills, but sometimes it is found on the gill operculum, the roof of the mouth, and on the pectoral and pelvic fins. For its identification, I am indebted to Professor C. B. Wilson. To the Commissioners of Fisheries of the State of Wisconsin, and their employes, especially Mr. Zalsman, foreman of the Wild Rose hatchery, my thanks are due for many courtesies shown me. To Professors E. A. Birge, George Wagner, and A. S. Pearse I wish to extend my best thanks for their many helpful suggestions.

II. DESCRIPTION OF THE FREE-SWIMMING COPOPOD

Lernaeopoda edwardsii, like all known species of the *Lernaeopodidae,* is parasitic during almost its whole life. The duration of its free-swimming existence is very short, perhaps not more than two days. Its nauplius and metanauplius stages are passed within the egg sac of the mother, and the animal hatches

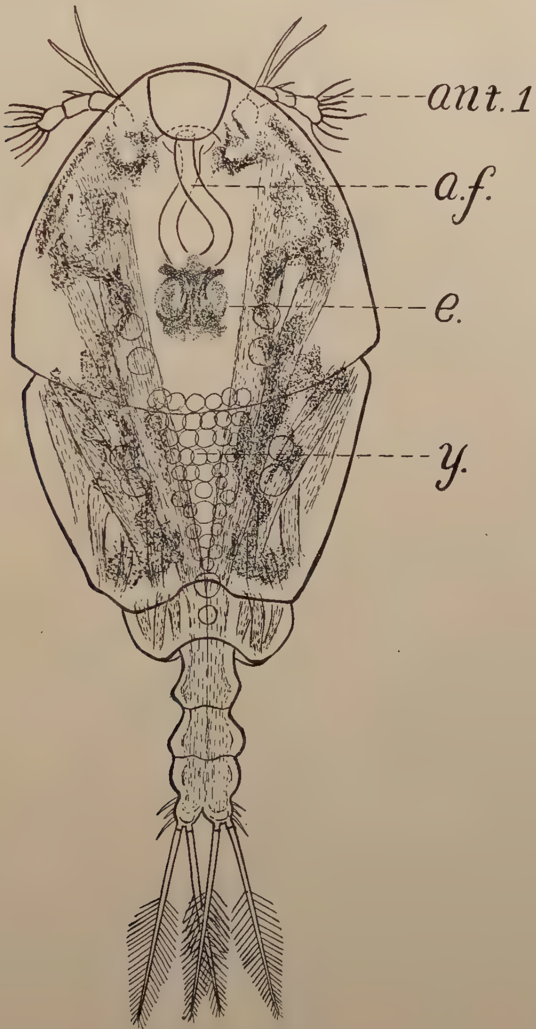

FIGURE 1. Lernaeopoda edwardsii. Dorsal view, free swimming stage, x 173.5
a. f. =attachment filament.
ant. 1=first antennae.
e =x-shaped eye.
y =yolk.

into a fully developed larval form, which immediately begins an active hunt for its host. During this stage of its life history the copepod does not feed, its nourishment being derived from the yolk which it carries over from its embryonic development (figure 1, y).

The larva is minute in size, about 0.726 m. m. in length. Running along each side of its dorsal surface are two well defined brownish streaks of pigment. A characteristic x-shaped copepod eye occupies the middle of the head (figure 1, e).

The head is broad, elliptical, and bears the mouth parts and a peculiar attachment filament. The mouth parts are situated on the ventral surface and consist of the first antennae, the second antennae, the mouth tube, stationed between the second antennae, the mandibles, the two pairs of maxillae (the first and the second), and the maxillipeds. The attachment filament is located beneath the head, and is made up of two parts:—(1) a broad circular, mushroom-like body whose position is between the first antennae, and (2) a tube-like structure, which makes its way backward from the posterior region of the mushroom body as far as the eye, and then turns upward in one circular loop, passing underneath the first part of the tube, and continues to ascend until it reaches the level of the posterior margin of the mushroom body, where it is attached to the head (figure 1, a, f).

The thorax has two segments and these bear the two biramous swimming feet (Fig. 2 s. f. 1 and s. f. 2), which end in broad laminated bases—the respective exopods and endopods. Each exopod terminates in four long feathery setae, whereas the endopods contain seven of these plumose structures. The feet are operated by a system of strongly developed dermal muscles situated along the dorsal side of the body.

The abdomen is rather slender and contains three segments. The last of these is supplied with four feather-like setae, as well as three pairs of smaller seta-like appendages, that are vestigial in character.

The head and the first thoracic segments comprise the main bulk of the copepod's body. Figures 1 and 2 illustrate, respectively, a dorsal and a ventral view of the free-swimming copepod.

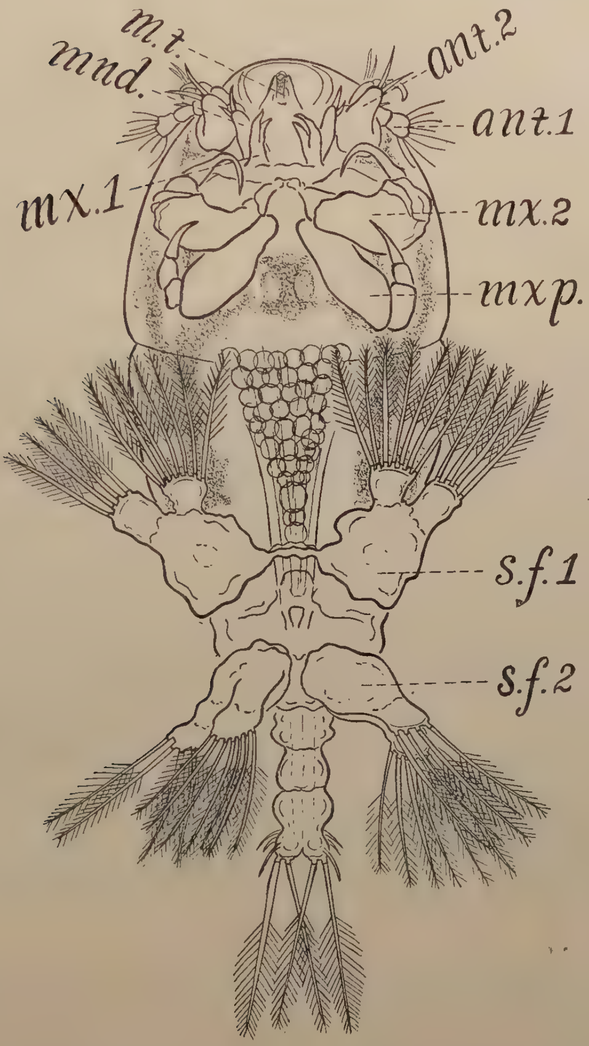

FIGURE 2. Lernaeopoda edwardsii. Ventral view, free swimming stage, x 173.5
ant. 1=first antennae.
ant. 2=second antennae.
mnd. =mandibles.
m. t. =mouth tube.
mx. 1=first maxillae.
mx. 2=second maxillae.
mxp. =maxillipeds.
s. f. 1=first pair of swimming feet.
s. f. 2=second pair of swimming feet.

III. HATCHING THE ORGANISM

In order to obtain enough material for experimentation, it became necessary to hatch the copepods artificially. The first efforts were confined to attempts to hatch the parasites in aquaria within the hatchery, but this proved a failure. Conditions here were far from normal, and the attempt was soon abandoned.

Outdoor experiments were next tried. Two large tanks were constructed, which were eight feet long by three and one-half feet wide and two and one-fourth feet high. The frame of these tanks was made of wood, while the sides consisted of coarse wire netting. The interior faces were lined with fine linen gauze so as to prevent the escape of any copepods. Figure 3 is a photograph of one of the tanks.

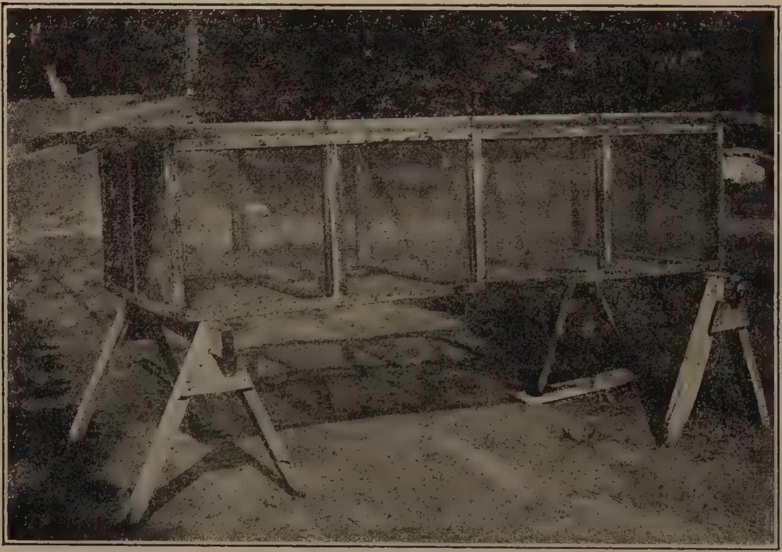

FIGURE 3. Hatching tank

Simply stationing these tanks in one of the open hatchery ponds proved insufficient, for, through lack of circulation, trout placed into them very quickly succumbed. So the tanks were placed in such a way that the water from some feed pipes ran directly into them. This arrangement proved entirely satisfactory. Figure 4 shows the manner in which the tanks were placed within the pond. The water can also be seen entering them.

Before putting any of the infected fish into the tanks; the water in the feed pipes was thoroughly examined in order to determine whether *Lernaeopoda edwardsii* existed in it. Fine linen bags were tied over the outflows, thereby catching the organisms brought in by the water. The contents of these bags were looked over under the microscope three times daily. Fifteen examinations of these catches did not reveal a single parasitic copepod, and this convinced me that the water was free from the infection. One hundred parasitized trout were next introduced into each tank, and the covers placed over them. Two days later, the first batch of free swimming larvae was obtained—about two dozen of them. This was on July 17th, and almost every day after that until September 5th, when the investigator left the hatchery, from a dozen to three dozen free swimming parasites were secured.

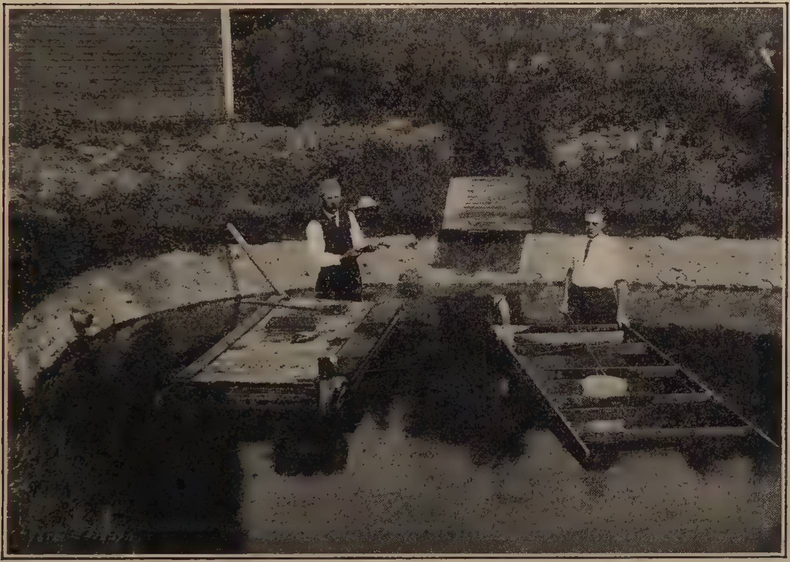

FIGURE 4. Tanks in position

The animals were scooped up with an open tow net, which was dragged along the surface of the water. The net had an aluminium cup attached to its tapering end. In the bottom of this cup there was an opening covered by a tightly fitting screw-cap. By unscrewing this cap, each haul could easily be transferred from the cup to another receptacle without losing any of the gathered organisms. Generally, each catch was strained through a fine linen plankton sieve, in order to condense the haul for examination. By means of a pipette the copepods were segregated from the other organisms, and introduced into a clean dish of water, where they were allowed to remain until needed.

IV. MOVEMENTS OF THE LARVAE UNDER NORMAL CONDITIONS

In the free living stage, the copepod swims about actively, with a snappy, dart-like spiral motion. Its mouth parts are, at the same time, moving incessantly, always ready to grasp their host and thereby insure the further development of the organism. Movement through the water is accomplished by the two biramous swimming feet on the thorax. In their normal resting attitude, the feet are held in an oblique position, with their setae pointed toward the head of the organism. The abdominal portion of the copepod is somewhat bent, at an angle of about 20° with the long axis of the body.

Motion is produced by the contraction of the powerful dermal muscles, which cause the swimming feet to dart backwards, thus shooting the organism ahead. The copepod, in its motion, passes through the same angle as that which the swimming feet traversed in the act of propelling the body. The actual distance covered by the copepod through one stroke of its feet is about an inch. Further motion is accomplished by a repetition of the same process; the animal thus travels in a snappy, spiral path (figure 5). When motion ceases, Lernaeopoda usually takes an upright position, with its long axis almost perpendicular to the surface of the water. Soon it turns upside down, and slowly begins to sink to the bottom, where it may assume a ventral or a dorsal position, depending entirely on which side of the body strikes the bottom first.

Oftentimes the copepod is found adhering to the side of the glass dish nearest the window, or it may sometimes suspend itself on the surface film of the water. In such cases, the larva maintains an upright position, while the first antennae are stretched out horizontally, making an angle of almost 90° with the long axis of the body. By means of these antennae the copepod is enabled to cling to the sides of the dish or to suspend itself from the surface film. In the latter case, surface tension undoubtedly plays the important rôle in maintaining the animal. Parker (1901), has observed similar behavior in the marine copepod *Labidocera aestiva*. He concluded that the antennae serve as means of attaching the copepod to fixed objects or to the water film. My observations are in accord with his.

The peculiar spiral movement of the copepod is of great significance. Many of the Protozoans and Rotifers have for a long time been known to move in this way. Jennings, more than any other investigator, has made a careful study of the problem, and has shown that a spiral path is of great adaptive value to the lower organisms. He has found (1901, '04, '06) that most of the Infusorians, especially the "hunter ciliates," move in a spiral course. In his work on Paramecium we get a thorough analysis of this type of locomotion. Discussing the adaptiveness of this movement, Jennings says:

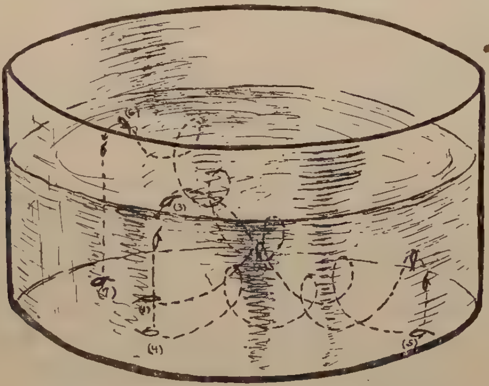

FIGURE 5. Normal movements of larva.

"The problem solved by the spiral path is as follows: How is an unsymmetrical organism, without eyes or other sense organs that may guide it by the position of objects at a distance, to maintain a definite course through the trackless water, where it may vary from the path to the right or to the left, or up or down, or in any intermediate direction? It is well known that man does not succeed in maintaining a course under similar but simpler conditions. On the trackless, snow-covered prairie, the traveler wanders in circles, try hard as he may to maintain a straight course, though it is possible to err only to the right or left, not up or down as in the water. Paramecium meets this difficulty by revolution on the axis of progression, so that the wandering from the course in any given direction is exactly compensated by an equal wandering in the opposite direction. Rotation on the long axis is a device which we find very generally among the smaller water organisms for enabling an unsymmetrical animal to follow a straight course. The device is marvellously effective, since it compensates with absolute precision for any tendency or combination of tendencies to deviate from a straight course in any direction whatsoever."

"The normal movements of Paramecium are adaptive in another respect. The same movements of the cilia, which carry the animal through the water, also bring it its food. Thus Paramecium is continually receiving samples of water in front of it. Since in its spiral course the organism is successively pointed in many different directions, the samples of water it receives likewise come successively from many directions. The animal is given opportunity to try the various different conditions supplied by the neighboring environment."

In the case of Lernaeopoda, we meet with a similar condition. The organism, like Paramecium and the other Infusorians, circles through the water in its characteristic way, "trying" the water, so to speak, in every direction. Of course, the animal being a parasite throughout most of its life, must come in contact with the proper host in order to carry on its further development. In other words, the copepod, like Paramecium, must meet its food in order to exist.

It is questionable whether the larva perceives objects through its ocellus. Even if it did, however, the visual range would, in all probability, be so short that the organism could not see its host in the water. It thus becomes a question of the copepod searching out its host by random movements, or perishing. Chance plays the greatest part in its ever meeting the host. The movements of the animal, therefore, are apparently adaptive. The copepod darts up and down, circles in this direction and in that. Its movements bring it into as many different localities as possible. If one path happens to bring it in contact with the necessary host, attachment immediately takes place, and the life of the individual and its progeny is secure. If, however, the organism does not meet the host, it tries other regions. The copepod perishes if its movements do not meet success within a given time.

V. REACTIONS TO CONTACT

Lernaeopoda is often found adhering to small bits of alga and other substances that float about loosely in the water. A glass rod or a needle may be slowly brought in contact with the body of the copepod, without producing the avoiding reaction. The organism may even adhere to the object for some period. When an object rapidly approaches the animal, it immediately shifts its position, thus avoiding the obstacle. Tapping or jarring a dish containing the copepod, even blowing on the surface of the water, or allowing a drop of water to fall directly above a resting copepod, calls forth the avoiding response; the animal quickly leaves its initial position and moves to other regions. When a copepod is picked up in a pipette and transferred to another dish of water, it almost always sinks to the bottom and remains motionless for a few seconds. Then it begins to dart about actively. In general, Lernaeopoda reacts positively to contact stimuli which are weak in character, whereas to strong stimuli it is negative.

VI. REACTION TO GRAVITY

Normally, Lernaeopoda responds positively to gravity. Its specific gravity is heavier than that of water, and it therefore tends to sink to the bottom. This was determined by the following experiment. Six copepods were placed in a test-tube filled with water and this was then tightly corked. When the tube was held in a vertical position, the organisms were observed to sink to the bottom, with their bodies almost vertical and their heads downward. As soon as they reached the bottom of the tube, the animals assumed a horizontal position, either ventral or dorsal, and began to move about actively. When the tube was reversed the larvae again sank to the bottom in their characteristic way. When the side of the test-tube was lightly tapped, while the copepods were passively sinking downward, they were observed to instantly dart upward again. However, as soon as the disturbing agent ceased acting, the animals again began to sink, until they reached the bottom, and here they moved about in their peculiar way. It becomes evident that this is not exactly a case of geotactic response but merely a result due to the high specific gravity of the copepod.

VII. REACTIONS TO LIGHT

1. *Behavior in daylight.*—Seven copepods were placed into a round dish of water, and allowed to remain near a window for some time. Soon all the organisms gathered near the window. Rarely did one leave the area. If a copepod, through its motion, happened to be brought into the opposite side of the dish, it soon began to adjust itself accordingly, swimming about actively until it was brought into the region of greatest illumination.

When a hand was passed between the window and the glass dish, the shadow caused the copepods to momentarily dart about. They did not, however, leave the most highly illuminated side of the dish, but actively moved about in it. The response in this case is similar to what Whitman (1898) has observed in the leech Clepsine. If a hand is passed over a dish containing a number of Clepsine, the shadow causes the animals to stretch in every direction, as if trying to reach something. Bateson (1887), has found that a passing shadow also causes a similar response in shrimps and prawns.

Obviously, this mode of behavior is of great value in procuring these animals their food. As Mast (1911) says, "The important point is that the shadow in itself is of no particular importance, but what follows may be."

In direct sunlight, the copepods were found to behave similarly. The reaction was observed many times and the positive phototropism was very striking.

2. *Behavior in artificial light.*—All experiments with artificial light were carried on during the evenings. The hatchery was situated a good distance from any of the neighboring dwelling houses, and it was also surrounded by tall trees, so that the laboratory was perfectly dark on the nights when experiments were conducted.

Five copepods were placed into a circular dish, eight and one-half inches in diameter, and this was allowed to remain in darkness for about an hour. The current was then switched on to a 60 c. p. Mazda bulb, which had previously been arranged in position about a foot from one side of the dish. When first illuminated, all the copepods were found to be at the bottom; but soon they began to dart about in every direction, ultimately making their way into the lighted area, where they remained. When the light was shifted to the opposite side of the dish, the organisms also changed their position. They moved about actively and in a few moments all had made their way across the dish, to the light side. An object, such as the hand, passed between the light and the dish, produced the same reaction as that brought forth by the shadow in ordinary daylight.

When an aqueous solution of alum was intercepted between the dish containing the free swimming copepods and the light, in order to absorb the heat from the rays, the organisms were found to behave similarly. Of course, the water in the dish served the same purpose to some extent. It is seen then that it is the light which causes the copepods to orient and not the heat produced by the electric bulb.

In another series of experiments twelve of the animals were used, and the same results were obtained. Here the electric bulb was slowly shifted in a circle around the dish, and the copepods slavishly followed the light. It is remarkable to note with what precision the organisms shift, when the position of the light is gradually changed. Time and time again, the animals made the complete round of the dish.

The definiteness with which the copepods orient to light is even more easily discerned when an oblong dish is used. Eight copepods were placed into a glass dish whose dimensions were eight inches long, one and one-fourth inches high, one and one-fourth inches wide, and were allowed to remain in the utter dark for about an hour. Then the current was switched on to a 60 c. p. Mazda globe, which was previously arranged in place at one end of the dish. The sudden flash caused the organisms to leave the bottom and to swim actively about in every direction. Shortly, however, they all made their way into the most highly illuminated region and remained there. Now a similar electric lamp, stationed at the opposite end of the dish, was turned on, while at the same time the first globe was extinguished. The copepods soon began to shift their position. One after another, they circled through the water, actively making their way from the dark side of the dish to the lighted region. In two instances, the organisms were timed. In the first case it took the copepods five minutes to traverse the entire length of the dish, while in the second instance the time was six minutes.

3. *Behavior in light of low intensity.*—In light of low intensity, the copepod does not react quite as definitely as in strong light. This was brought out by the following experiment. An oblong glass dish was used, whose dimensions were the same as those of the oblong dish used in the previous experiment. Eight copepods were placed into it, and with a 60 c. p. Mazda lamp these were attracted to one end. Then the current was turned on to a 1 c. p. bulb stationed at the opposite end, while at the same time the other globe was extinguished. But the organisms paid little attention to the faint glimmer. Two or three of them were observed to travel a very short distance to the light, but no definite orientation occurred. When a 4 c. p. bulb was substituted for the 1 c. p. lamp, the same behavior resulted, no specific orientation taking place. If, however, an 11 c. p. globe was switched on, the animals oriented definitely, but slowly. They all moved to the illuminated side of the dish. A 16 c. p. bulb brought about this reaction more readily, and globes of higher intensity increased the positive behavior accordingly.

From these observations it becomes evident that the definiteness of orientation of the copepod varies with the intensity of illumination. Any increase in the illumination brings about a corresponding increase in precision of the specific reaction of the animal. Yerkes (1900), has noticed a similar behavior in Daphnia and Cypris.

The above experiments tend to bear out what was observed concerning the behavior of the copepods in their normal surroundings. While conducting hatching experiments it was noticed that whenever the covers of the hatching tanks were removed, the copepods would suddenly bob up to the surface of the water from underneath. This was observed many times and the regularity of its occurrence was very striking. The only explanation that could be found for this behavior was that the increase of illumination within the tanks attracted the animals to the surface. With this in mind, the foregoing series of light experiments was undertaken. The results have convinced me of the fact that in ordinary daylight, especially in sunlight, the free swimming copepods move about close to the surface waters. In weak light, and in total darkness they sink passively to deeper regions.

The migrations of water dwelling organisms is a problem that has been studied by a number of investigators. Giesbrecht (1892), in his splendid report on the pelagic copepods of Naples, states that Weismann (1877), was the first one to attribute the upward and downward movement of pelagic organisms to the responses of these animals to light of different intensities. However, the first investigators to determine this question experimentally were Groom and Loeb (1891), who worked on the nauplii of the barnacle *Balanus perforatus*. In the laboratory, these investigators found that when the young were subjected to light of strong intensity, they reacted negatively, whereas in faint light, they were positive. These reactions were similar to the behavior of the nauplii in the open sea, where the larvae are found clinging to the surface of the water at night only, while during the day they swim about in deeper regions. Based on these observations, Groom and Loeb came to the following conclusion: "Das starke Licht bei Tage treibt die Tiere in die Tiefe, das schwache Licht, das auch in der Nacht vom Himmel ausgesandt wird, zwingt sie wieder in die Oberfläche emporzusteigen."

Loeb (1893) has brought forth additional evidence among marine copepods as well as other animals, such as Limulus and the Annelid Spirographis, which tends to strengthen the theory that light causes the periodic migrations of pelagic organisms. In this paper, however, Loeb calls attention to other factors besides light, such as gravity, which may also play an important part in determining these periodic movements.

Parker (1901), in his studies on the daily migrations of the marine copepod *Labidocera aestiva*, found that light was the most important factor in the vertical movements of these organisms. "*Labidocera aestiva* frequents the surface of the sea from sunset to sunrise. From sunrise to sunset, it is presumably in deeper waters. Its migrations are explained as follows: Females rise to the surface with the setting sun, because they are positively phototropic to faint light and negatively geotropic; they descend into deep water with the rising of the sun, because they are negatively phototropic to strong light (their negative geotropism being overcome by their negative phototropism); the males follow the females in migration, because they are probably positively chemotropic toward the females."

Juday (1904), has studied the diurnal migrations of fresh water Plankton Crustacea, and found that most of these organisms come to the surface of the water at night, especially during the early part of the evening. Through most of the day, however, the animals occupied deeper water. He calls attention to the fact that diurnal movements are rather complex phenomena, and that they cannot be attributed to a single factor alone. Each lake presents different conditions, and these modify the behavior accordingly. The downward movement of the Plankton Crustacea he attributes to light, but he maintains that other factors, such as temperature, food, and the substances dissolved in the water may control the upward migrations of the animals.

Esterly (1907), working with Cyclops also emphasizes light as the directive agent in the migrations of this form.

It is thus seen that amongst marine as well as fresh water organisms we find a periodic migration. Light seems to play the most important factor in these movements. We must not, however, leave out of consideration such important factors as food, temperature and gravity, for these may also influence migrations, as was shown by Loeb (1893), Parker (1901) and Juday (1904).

In the case of Lernaeopoda we meet with an organism that offers an exception to the general rule of vertical migrations. Here we find the larva attracted by strong light, and it swims about close to the surface of the water during the day time, even overcoming its natural tendency to sink downward. At night, on the other hand, the animal does not react to weak light, and responds to the pull of gravity, thereby sinking to deeper regions. Clearly this behavior is of great value to the stability of the species. The migrations of the copepod are identical with the movements of its host. During the day trout generally feed near the upper surface of the water, whereas, at night they frequent lower regions.

VIII. REACTIONS TO HEAT

Loeb (1893), while experimenting with the copepod *Temora longicornis*, found that increasing the temperature of the water caused positively phototropic individuals to become negative, and vice versa; decreasing the temperature of the water brought about a change in normally negative individuals and caused them to become positive. Holmes (1901), found that increasing the temperature hastens, or may even induce, positive reactions among certain amphipods. This same author (1905), also found that an increase in temperature caused Ranatra to accentuate its positive phototaxis, while a decrease tended to produce the negative reaction. Yerkes (1900), could not induce any changes in the behavior of Daphnia and Cypris to light by varying the temperature. Parker (1901), also met with no success when he tried to induce changes in the light reactions of Labidocera by similar methods.

In the present experiments with heat, it was found that increasing the temperature of the water caused no change in the light reaction of Lernaeopoda. Six copepods were placed in an oblong dish of water, whose temperature was 58° F. These were then attracted to one end of the receptacle by a 60 c. p. Mazda lamp. At the opposite end, water that had been heated to near the boiling point was slowly poured at intervals a few minutes apart. As soon as the warmer water reached the animals they became very active, darting about rapidly; but none of them left the illumined side of the dish. As more hot water was supplied, the movements became slower, until at the temperature of 81° F. all of them were dead in the region of positive phototaxis. It was thus seen that increasing the temperature does not alter the behavior of the copepods to light.

IX. REACTIONS TO CHEMICALS

The effect of chemicals was next tried, with two purposes in view: first, to determine whether chemicals could reverse the behavior of the copepods to light, and second, to find out the solution of the chemical necessary to kill the parasitic organism while in this free-swimming stage of its existence. Only the first of these problems will be discussed here. The other will be dealt with in another paper on the economic aspects of *Lernaeopoda edwardsii.*

The chemical experiments were all performed at night, when the only source of illumination was a 60 c. p. Mazda globe stationed about a foot from the receptacle containing the copepods. Most of them were also confirmed in diffuse day-light. The observations were made in oblong glass dishes whose dimensions were eight inches long, one and one-fourth inch wide, and one and one-fourth inch high. The number of copepods used in each case was four or more.

Before applying a reagent, the copepods were first attracted to one end of the dish and then the chemical was slowly poured, drop by drop into the opposite end of the vessel. The following table gives a condensed statement of the results obtained. The sign + is used whenever the copepods reacted positively to light, whereas the sign — is used when the reaction to light was negative.

Chemical used	Lowest percentage of chemical causing death	Time required to kill copepod	Behavior to light until death
Sodium chloride	1.2	15 min.	+
Potassium chlorate	0.2	4 "	+
Calcium chloride	0.85	4 "	+
Hydrochloric acid	0.08	2 "	+
Sulphuric acid	0.015	3 "	+
Tartaric acid	0.45	2 "	+
Oxalic acid	0.3	2 "	+
Copper sulphate	0.2	5 "	+
Acetic acid	0.1	3 "	+ (indication of reversal)
Nitric acid	0.03	16 "	+ (indication of reversal)
Magnesium sulphate	1.6	45 "	2+, 2—
Hydrogen peroxide	9.0	18 "	—

Copper sulphate was found to affect the copepods differently during the day than at night. In the dark room a solution of 0.2 per cent copper sulphate caused all the copepods to die in about five minutes. In daylight, however, a two per cent solution of the chemical affected the animals very little. After remaining in this medium for twenty minutes they appeared to be as active at the end of this time as at the beginning. When the solution was increased to three per cent the organisms died in about four minutes. Evidently these differences in the behavior of the free swimming copepods depend upon differences in their physiological states, which may perhaps have been due to minute differences in the environment of the animals at the times when they were secured; perhaps the individuals used during the day were younger, and therefore possessed greater vitality.

In acetic acid, nitric acid, magnesium sulphate and hydrogen peroxide the copepods gave indications of reversal in their behavior to light.

Acetic acid.—Acetic acid was slowly added until the water became a 0.1 per cent solution of the chemical. As the acid reached the copepods they became very active. One of them circled clear across the dish from the side nearest the light to the opposite end. The next moment, however, it moved into the light again, where it remained till death. In three minutes all of the copepods died in the illuminated region.

Nitric acid.—This chemical was slowly added to a dish of water containing four copepods. When the medium became a 0.03 per cent solution, the animals became very active, darting rapidly about in the light for nearly ten minutes. Then two of them died, while the other two moved a little towards the opposite side. The latter reaction was but momentary, however, and the copepods again returned to the illuminated region. One now began to move away from the lighted side, but when it traveled about one-third the distance it returned into it again and remained there till death. No actual reversal took place although there were very strong indications of the organisms trying to avoid the chemical.

Magnesium sulphate.—These observations lasted from 8.22 P. M. to 9.10 P. M. When the magnesium sulphate was added to the water gradually, the copepods remained positive until the concentration reached one per cent. Here the addition of the chemical was suspended, and after a wait of a few moments, one copepod was seen making its way from the lighted region, while the others kept moving about within it. When a card was suddenly flashed between the dish and the light, the passing shadow caused the negative copepod immediately to become positive again. When more magnesium sulphate was added until the solution was 1.6 per cent, two copepods died, while the other two became negative. Passing a shadow between the light and the dish brought them back again into the positive region, but as soon as this ceased, they again became negative.

One persisted in remaining here, while the other copepod darted back into the lighted side of the dish. About three minutes later the organisms died.

The following evening this same experiment was repeated. When the concentration reached 1.7 per cent, two copepods became negative. One of these became positive again. The concentration of the solution was now increased until it reached a strength of four per cent, but the copepods behaved as before, one remaining negative, while the others were positive. Every now and then one of the positive three would dart away from the light, but the next moment it would again become positive. The copepods were not killed in this solution in thirty minutes. We thus meet a parallel with that noticed in the discussion of the reaction to copper sulphate,—a difference in the physiological state of the copepods.

Hydrogen peroxide.—This chemical caused a distinct reversal in the behavior of the animals to light. When the water became a nine per cent solution of the chemical, all of the copepods, which up to this time had been darting about in the lighted region, suddenly reversed their direction and began to move away from the light. One died almost instantly, while the other three traveled about three-fourths the length of the dish. The motion of these copepods now became very slow; their dorsal muscles were affected to such a degree that the swimming feet could no longer beat with enough force to propel them through the water. The mouth appendages also stopped moving, and fifteen minutes later the copepods died.

From these results it becomes evident that the chemicals used have little effect on the behavior of the copepods to light. In a few cases a reversal in the orientation was observable. This was produced by the addition of hydrogen peroxide, magnesium sulphate, nitric and acetic acids. In the last three cases, however, the reversal may have only been incidental, for but one or two of the copepods became negative while the others remained positive. Generally those that did become negative remained in this region but a short while, and soon returned to the illuminated territory. In all the tests, when the chemical reached the animals they became very active, as if trying to get away from something that was affecting them severely. But as the concentration of the medium was gradually increased, the motion of the copepods became slower, until death finally overtook them in the lighted side of the dish. The organisms are so strongly positive in their reaction to light, that they persist in going toward the source of greatest illumination, even though they are brought into regions that are dangerous to their existence.

X. INFECTION EXPERIMENTS

In the hatchery ponds, as well as in the natural streams *Lernaeopoda edwardsii* was found to attack the brook trout only. A great many rainbow trout as well as German-brown trout were examined and not a single case of infection by the copepod was observed. Furthermore, suckers that were kept in the hatchery ponds, as well as those thriving in neighboring trout streams were examined, but were found to be clean and healthy. Now the question arose: What explanation could be offered for this choice on the part of the copepod for the brook trout only? In attempting to determine this a series of infection experiments were undertaken.

Three groups of three copepods were placed into three separate dishes of water. Into each dish was then placed, respectively, the gills of freshly killed brook, rainbow and German-brown trout. The fresh blood of the gills soon began to diffuse in the water and the behavior of the copepods was noticed. The copepods in the first dish into which the gill of the brook trout was thrown, became very active, darting about in every direction, as if they were in search of something. In the other two dishes, which contained the gills of the rainbow and German-brown trout, no such reactions of the copepods were noticeable. Two of the animals came in contact with the brook trout gill and began to attach themselves. In the other two dishes no attachment took place, in spite of the fact that the organisms came in contact with the gills a number of times.

The manner in which the copepod attaches itself to the gills of the brook trout is very interesting. Wilson (1911), in his paper on the development of *Achtheres amblophitis* Kellicott, a copepod of the family Lernaeopodidae, parasitic on the gills of the rock bass, describes the attachment of the organism as follows: "Of course, it is practically impossible to actually witness the fastening of the larva. But what has been observed in the chalimus larva of the Caligidae, we can infer what occurs here. The outer end of the attachment filament is enlarged into the mushroom form already described, and is filled with adhesive fluid. It lies just inside the frontal margin, covered only by a very thin outer cuticle. Doubtless, the larva rubs its frontal margin against the skin of the gill arch of its host and in this way burrows through the slime and outer integument to the solid tissue underneath, holding on meanwhile with its powerful maxillipeds. At the same time the thin covering of the frontal margin of the parasite is broken through and the end of the filament is brought in contact with the gill arch, to which it adheres firmly. By moving away from the point of attachment the coiled filament is drawn out of the body of the larva. As it comes forth the larva grasps it between the claws at the tip of the second maxillae."

This process of attachment as surmised by Wilson, however, was not found to be the method by which *Lernaeopoda edwardsii* attaches itself to the gills of the brook trout. By the aid of the microscope I observed the process of attachment four times. As soon as the copepod comes in contact with the filament of the gill, its mouth parts are inserted into the flesh, and by means of the powerful claw-like second maxillae it begins to rasp the filament until it forms a cavity within it. As soon as this occurs, the anterior portion of the copepod's head, the frontal margin, is brought in contact with the cavity and the enclosed attachment filament is injected into the hole. The spherical mushroom body adheres to the flesh and the regenerating tissue of the gill soon encloses it tightly, thereby fastening the organism firmly. The mouth parts are then withdrawn from the flesh of the gill filament. In this condition the parasite remains attached for a short time. Then the second maxillae detach the posterior region of the attachment filament from the head margin and they themselves become permanently attached to this end of the filament. Degeneration soon sets in and the organism changes considerably. The female copepod remains thus attached throughout life, while the male remains attached in this way until shortly before it is mature for copulation.

Wilson believes that the transference of the filament from the frontal margin to the tips of the second maxillae takes place at the time of fixation to the host, and that the larvae are never

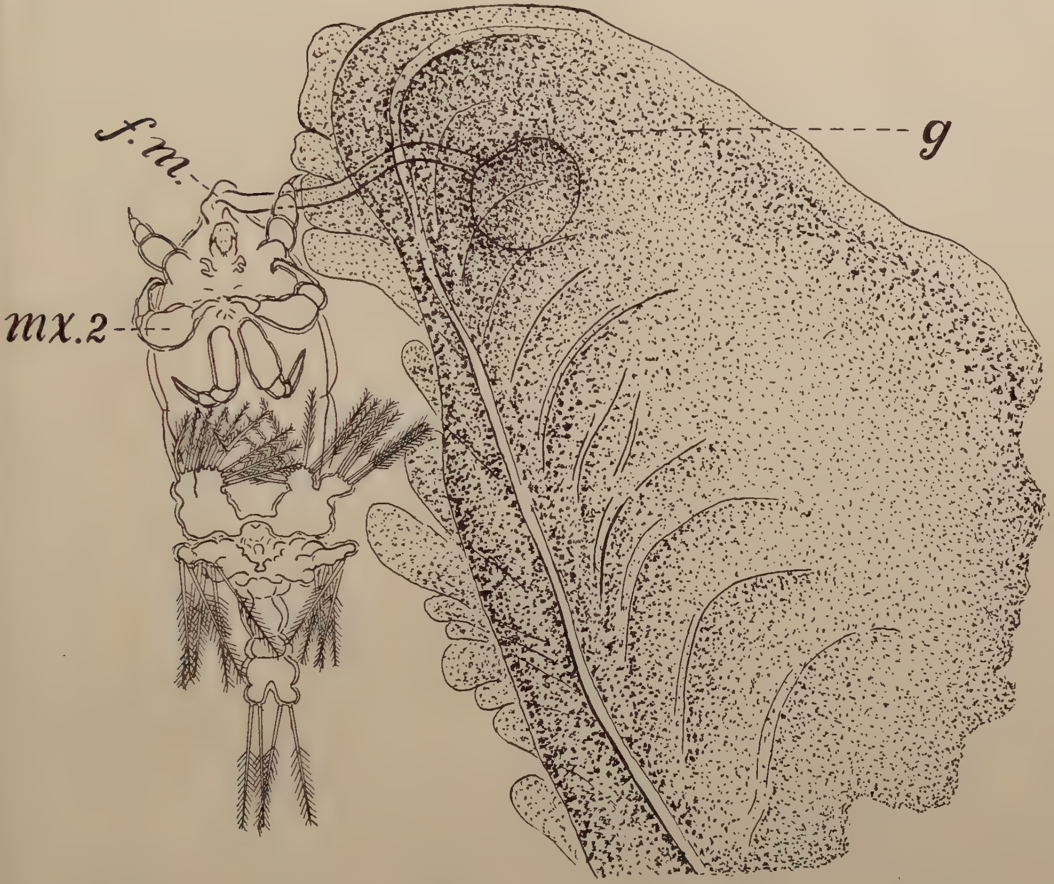

Figure 6. Lernaeopoda edwardsii. Larva attached by frontal margin, x 110
f. m. =frontal margin.
g. =gill.
mx. 2=second maxilla.

found fastened by their frontal margins. Figure 6 is a camera lucida drawing of a larva of *Lernaeopoda edwardsii* thus attached.

Let us now come back to the infection of the fish. In order to study the problem further, a floating cage was sunk in one of the hatching tanks, and into it were placed healthy specimens of brook trout, rainbow trout and perch. The fish were examined two days after the sinking of the cage and the brook trout were found to be the only species infected; the others were all clean. Five days later the perch died, but their gills revealed no infection by Lernaeopoda, their death was apparently due to a fungus which had developed on them. The rainbow trout were also found to be free from the copepod.

Lefevre and Curtis (1912), in their recent paper on the artificial propagation of fresh water mussels, note a similar preference on the part of the hookless glochidia of the genus Lampsilis for certain fishes. However, they have found that the glochidia may attach themselves to a number of different kinds of fish, although their choice for one is generally predominant. The glochidia are therefore not quite as exclusive in their choice as are the free swimming Lernaeopoda. The reactions observed in the glochidia and in the copepod are, undoubtedly, chemical in nature. In the case of the copepod there must be something in the blood or other secretions of the brook trout which attracts the parasite to this species of fish. This chemical substance, or substances, must be wanting in the other fish and they are, therefore, not parasitized by *Lernaeopoda edwardsii.*

XI. CONCLUSIONS

From the foregoing discussion it becomes evident that *Lernaepoda edwardsii* is well adapted to its parasitic mode of life. It moves about with a darting spiral motion, thereby covering a maximum of territory with the amount of energy it expends. In many respects this method of locomotion is similar to that of the hunter ciliates. The organism is so strongly attracted by intense light that during the day it frequents the upper regions of the water, though it is normally positively geotropic. In this position the copepod is very favorably situated, for the brook trout feed near the surface waters throughout most of the day, and hence the parasite is readily accessible to them. At night, on the other hand, the copepods are no longer attracted by light, and since they possess a greater specific gravity than the water, they passively sink to deeper regions. Here, also, their position is advantageous because after sunset the trout frequent the lower strata of water, and they are thus stationed close to the parasites where infection may occur and the life of the copepod thus insured.

XII. SUMMARY

1. *Lernaeopoda edwardsii* is a parasitic copepod which attaches itself to the gills of the brook trout. It attacks this species of trout only, the rainbow as well as the German-brown trout being immune from it. Undoubtedly, its reaction to the brook trout is a chemotactic one.

2. The free-swimming existence of the organism is very short, about two days at the most, and during this stage of its life history it swims about with a darting spiral motion.

3. When the copepod stops moving through the water, it sinks to the bottom in an upright position, with its head down. When it strikes bottom it may rest either on its ventral or dorsal side, depending entirely on which side of the animal strikes the bottom first. Undoubtedly the organism sinks because its specific gravity is greater than that of water.

4. Lernaeopoda is strongly positive in its reactions to intense light. In light of low intensity, however, it is indifferent. Because of its affinity for strong light, the copepod moves about near the surface of the water during most of the day. At night, the animal remains indifferent to weak light, and through its specific gravity it sinks to deeper waters.

5. Increasing the temperature of the water does not change the behavior of the organism to light.

6. Some chemicals have little effect on the behavior of *Lernaepodao edwardsii* to light. No reversal in the positive behavior of the larva could be induced through the use of sodium chloride, potassium chlorate, copper sulphate, calcium chloride, hydrochloric, sulphuric, tartaric and oxalic acids. In hydrogen peroxide, magnesium sulphate, nitric and acetic acids indications of reversal were noticeable.

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THE REACTIONS OF CERTAIN DERMESTIDAE TO LIGHT IN DIFFERENT PERIODS OF THEIR LIFE HISTORY

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PHOTOTACTIC REACTIONS OF *TROGODERMA TARSALE*, A MUSEUM PEST

While working on the life history and habits of T. tarsale[1] I made some observations which suggested the idea that it would be an advantage to know the exact phototactic reactions of this beetle in the different periods of its life history. Careful observations were made and it was noticed that the larvae immediately after hatching evince a markedly negative reaction to light by concealing themselves in any available shaded areas. If placed near a window they at once begin to crawl away from the light, and the reaction is even more pronounced when the specimens are taken into a dark room and a strong light is introduced at one end of the glass dish containing them. This negative response persists throughout their larval life. Before passing into the pupal stage their negative reaction is especially pronounced. Thus, the pupae are almost invariably found in dark places which afford them a favorable means of protection.

After metamorphosis, the adults, both male and female, retain the negative phototaxis. As a rule the insects remain for some time within the feeding material or cabinet in which they were reared. A large number of newly emerged adults were taken into a dark room and both sexes manifested a decidedly negative response to light of various intensities. During the sexual excitement which follows a day or two later they still remain negative. The female remains markedly so until her eggs are safely deposited. Several hours later, or the day following the egg-laying, the negative reaction is gradually inhibited until the insect becomes quite indifferent, and finally decidedly positive even to intense light. The males, too, during the last days of their lives become indifferent to light and often even strongly positive in their phototaxis.

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[1] Wodsedalek, J. E. "Life History and Habits of Trogoderma Tarsale, a Museum Pest." Annals of the Entomological Society of America, vol. 5, No. 4.

Although ordinarily the adults remain till death occurs in the cabinets where they had developed, not infrequently do we find some of them on the windows in the rooms where they make their abode. A number of such specimens were at different times collected and dissected, but in no cases were there any eggs found within the bodies of the females. This also indicates that they lay their eggs before they become positively phototactic and desert their places of concealment, and apparently their destruction at this time is futile.

PHOTOTAXIS IN THE CARPET BEETLE OR "BUFFALO MOTH" (*ANTHRENUS SCROPHULARIAE*), AND ITS ECONOMIC IMPORTANCE

In view of the results obtained through the observations and experiments on light reactions in T. tarsale, an idea suggested itself that the light reactions in other Dermestidae might be worked out to some economic advantage. The popular belief in the case of the common carpet beetles is that the pests metamorphose in the houses and immediately go outside to breed, where they are often very abundant on flowers, and that after this is accomplished the females return to the houses to lay their eggs. Careful observations and experimental work with this species, however, revealed facts contrary to the common belief.

In the spring of 1911 about six hundred adult specimens were collected from the blossoms of Spiraea on the University of Wisconsin campus. More than a hundred of the female individuals were killed and dissected, but no eggs were found within their bodies. The remaining insects were kept in the laboratory with an ample supply of food with the view of obtaining some eggs. The jars containing the beetles were carefully examined but no eggs were secured. After the specimens had all died, the jars were put in a convenient place with the idea that possibly some eggs had escaped the writer's notice and that in time some young larvae would probably appear; but not a single individual was obtained.

A similar process was repeated in the spring of 1912. This time, however, the beetles were not as numerous on the flowers of Spiraea as they were the previous season, a fact probably due to the cool, rainy weather. About sixty female insects were dissected and over two hundred specimens of both sexes were kept alive for further observations. Again no eggs were procured. Not a single case of copulation was observed during the process of collecting about a thousand individuals in the two successive seasons. In the laboratory where the collected beetles were kept with an abundance of food and where most of them lived from five to fifteen days, again no evidence of sexual excitement was observed.

The same season I succeeded in getting a number of almost full grown larvae and also a number which were about half grown. The large specimens pupated and metamorphosed the first part of June and produced a new generation, the larvae of which were kept for further experimentation. The smaller larvae matured and reproduced in fall.

Experiments on light reactions were performed and, as in the case of T. tarsale, it was found that A. scrophulariae larvae are decidedly negative to light in all stages of their larval history. Also both sexes of this species manifested a decidedly negative reaction to light immediately after their emergence from the pupal skins. This response persisted through the period of fertilization and egg-laying. Very shortly after laying their eggs the female insects reversed their reaction to light, becoming decidedly positive. The males, too, completely reversed their phototaxis during the latter part of their lives. When the beetles were placed near a window they made frantic efforts to get outside. The same reversal was observed in experiments with an electric light in the dark room. Similar results were obtained with the specimens of the second annual generation which metamorphosed in fall.

L. O. Howard,[1] in his paper on the Carpet Beetle or "Buffalo Moth," says that it is probable that the migration of this beetle from the house takes place, under ordinary circumstances, after the eggs have been laid. The foregoing facts show conclusively that the Carpet Beetles lay their eggs before they desert the houses. When their phototaxis is reversed they are attracted to the windows by the light and make their escape if possible. When they reach the open air they are attracted by certain flowers, particularly of the family Scrophulariaceae. The blossoms of Spiraea on which they may be found by the thousands here in Madison, are also strongly attractive to the beetles. It is very probable that they spend the remainder of their lives on the blossoms, never returning to the houses. At any rate, they are harmless at this stage and if eradication would be effected they must be destroyed before they lay their eggs.

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[1] Howard, L. O. The Carpet Beetle or "Buffalo Moth" (Anthrenus scrophulariae). Circular no. 5, revised edition, U. S. Dept. of Agric., Bureau of Entomology. This circular suggests some remedies for the checking of the pest which may also be applied to T. tarsale.

THE BLACK CARPET BEETLE (*ATTAGENUS PICEUS*)

The black carpet beetle, another of the Dermestidae, possesses habits somewhat similar to those of A. scrophulariae and T. tarsale. Observations and experimental work on this species seem to indicate that it behaves practically the same in its phototactic reactions as do the other two beetles mentioned. However, I have been able to secure only a small number of specimens of this species and the results obtained, therefore, are not entirely conclusive as in the case of T. tarsale and A. scrophulariae, both of which were obtainable in large numbers.

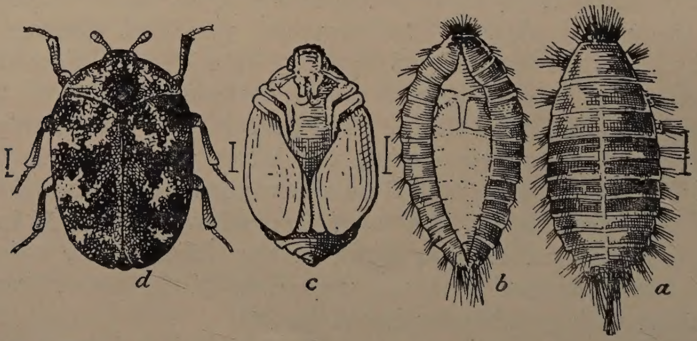

Figure 1. The carpet beetle (*Anthrenus scrophulariae*): *a*, larva, dorsal view; *b*, pupa within larval skin; *c*, pupa, ventral view; *d*, adult. All enlarged (from Riley).